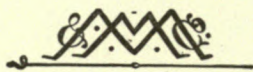# ATLAS OF NERVE CELLS

ATLAS OF NERVE CELLS

BY

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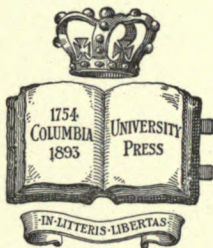WITH THE CO-OPERATION OF

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WITH FIFTY-THREE PLATES AND THIRTEEN DIAGRAMS

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PREFACE

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IT is the object of this atlas to present to students and teachers of histology a series of photographs showing the appearance of the cells which form the central nervous system, as seen under the microscope. These photographs have been made possible by the use of the method of staining invented by Professor Camillo Golgi of Pavia. This method has revealed many facts hitherto unknown, and has given a conception of the structure and connections of the nerve cells both novel and important. In the light of these facts it has been necessary to discard many of the views previously taught by anatomists, and to revise some of the physiological and pathological data supposed to be fundamental.

The nervous system is now known to be composed of a vast number of independent units, called neurons, which consist of a cell body with two varieties of branches called dendrites and neuraxons. The cell bodies vary in size, shape, and appearance; their dendrites, formerly known as protoplasmic processes, present great differences in form, length, and manner of subdivision; their neuraxons, formerly called axis cylinder processes and believed to have no branches, are now known to give off many little collateral offshoots as important as the main trunk.

The arrangement of these neurons varies greatly in different parts of the nervous system. In the spinal cord they are collected into groups arranged in a long cylindrical column. In the cerebral axis they are scattered among the various nerve tracts as well as collected into separate groups. In the basal ganglia they are gathered into large masses separable into divisions. In the cortex of the cerebrum and cerebellum they are spread out into thin but very extensive layers containing a great variety of cells.

The interrelation of these neurons is also a subject of importance which recent researches have demonstrated satisfactorily for the first time. The old theory that the processes of adjacent cells joined together, forming everywhere a fine network of nerve fibres within the gray matter, has been discarded. For the method of Golgi has shown that each cell is an independent entity, its branches and subbranches of both varieties preserving their identity from origin to ending, interlacing, it may be, with those of other cells, as the branches of trees in a forest may interlace, but really as distinct and separable from each other as are those trees with their twigs and leaves.

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In the most recent text-books of neurology and in the atlas of Golgi these facts have been shown by drawings and diagrams. But all such drawings are necessarily imperfect and involve a personal element of interpretation. It has seemed to me, therefore, that a series of photographs presenting the actual appearance of neurons under the microscope would be not only of interest but also of service to students. The Golgi method lends itself very readily to the photographic process, for the cell with its dendrites and neuraxon is stained black upon a light yellowish ground, and thus is capable of giving a sharp picture. In the preparation of this atlas I have had the coöperation of Dr. O. S. Strong, who has cut and stained the specimens, and of Dr. Edward Leaming, whose skill in photography has made this work possible. Dr. Strong has been able to produce remarkably successful sections of the various parts of the nervous system, both brain and spinal cord, and has made some valuable modifications of Golgi's methods. He has contributed a section upon the technique containing many original and important suggestions. In the art of photographing microscopic specimens Dr. Leaming has been particularly successful. It can be readily imagined that the difficulties of obtaining a clear picture focussed in one plane upon the photographic plate are at times almost insuperable, the microscopist ordinarily bringing various planes into his vision by the aid of the fine adjusting screw of the instrument. By care in the selection of specimens, by ingenious contrivances to insure a perfect focussing, and by the use of various methods adapted to each emergency, Dr. Leaming has succeeded where others have failed. He has contributed a section of much value upon the photographic technique. The photographs have been reproduced in a painstaking manner by Mr. Edward Bierstadt, whose process of artotyping has been selected after a careful comparison with other methods of reproduction; and it can be justly said that they show every detail of the original photographs.

In preparing this atlas I have not attempted to write an exhaustive account of nerve histology, but rather to present a brief review of the essential facts which can be demonstrated by the aid of the Golgi stain, and to show how these facts aid in the knowledge of nervous action. There are other methods of investigation, notably the method of Nissl, which cannot be demonstrated by photography, and which reveal facts of equal importance, but these must be sought elsewhere. I may be permitted, however, to point out that this atlas is based mainly upon preparations from the human nervous system; that it not only includes the spinal cord, cerebellum, and brain cortex, which have been studied by Golgi, Cajal, Van Gehuchten, Retzius, and Lenhossék, but also presents original studies of the corpora quadrigemina, optic thalamus, and lenticular and caudate nuclei, and is thus quite complete in its scope. It is my intention at some future time to issue another volume which will include the peripheral nerves and their terminations and the organs of sense.

M. Allen Starr.

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THE HISTOLOGICAL TECHNIQUE

By OLIVER S. STRONG, M.A., Ph.D.

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THE Golgi methods of staining nerve cells and their processes are known as impregnation methods in which metallic salts are precipitated in or around the elements, thus bringing them into clear relief. The nerve cell and its processes appear as a black silhouette upon a yellowish or whitish ground. Golgi has employed both silver and corrosive sublimate methods. It is the former only which have been used in the preparation of the specimens shown in this atlas.

In the silver methods the tissue is first hardened in a solution of potassium bichromate and then brought into a solution of silver nitrate. If the tissue is in the proper stage of hardening, the silver is deposited (probably principally in the form of silver chromate) in and around certain of the nervous elements. As the remainder of the tissue remains unstained the sharp contrast thus afforded enables one to trace the finest ramifications of the nervous elements impregnated.

It is a peculiarity of these methods that all the elements present in the tissue are very rarely impregnated at one time, and those elements which are thus picked out by the stain are more or less different in each preparation. Owing to this peculiarity, the various nerve cells with all their processes can be distinguished separately. Were all the cells and processes present stained at once, there would be simply an inextricable mass of black-stained cells and fibres.

The silver methods may be subdivided as follows:

(a) *Golgi's long method*, in which potassium bichromate alone is used in hardening the tissue before placing it in the silver nitrate. This process requires nearly a month to harden the tissue properly.

(b) *Golgi's rapid method*, in which a mixture of potassium bichromate and osmic acid is used to harden. Here the time required is reduced to a week or less.

(c) *Golgi's mixed method*, in which the tissue is placed first in potassium bichromate for from a few days to a month and then in the osmic-bichromate mixture.

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For all these methods we are indebted to Professor Camillo Golgi, of Pavia. The rapid method is the most important, and is the one which is now so extensively used. It is especially applicable to embryonic tissue, to nerve endings, etc.

In addition to the above, the writer has devised two modifications which are quick and yet avoid the use of osmic acid, which is an expensive reagent and difficult to manage; viz.:

(d) The *lithium bichromate* method, in which *lithium* bichromate is used instead of potassium bichromate. The results resemble those of the long method, but the time of hardening is reduced from nearly a month to two days.

(e) The *formalin-bichromate* method, in which a mixture of potassium bichromate and formalin (= 40 % solution of formaldehyde) is used in hardening. This also requires little time to harden. It is more certain than (d). Both (d) and (e) are especially applicable to adult brains.

The actual method of procedure in making the preparations for the atlas will now be given. Certain of the details were rendered necessary by the nature of the material and by the fact that the preparations were to be photographed.

It will be most convenient to deal first with the preparations made from human embryos and by means of the rapid method, as these constitute the bulk of the preparations used.

The first essential is that the material be tolerably fresh. All the material which yielded good results was obviously, from its general appearance, in good condition. Exact data are not available, but in general human embryos of seven and eight months, if kept cold, probably remain in fairly good condition for at least 24 hours after death.

The hardening process. — If the entire embryo is at hand, two courses are open: the brain may first be injected *in situ* with hardening fluid, or may be immediately removed and suitable pieces placed in the fluid. Injection was tried on one brain only, but the results warrant its further trial. In this case the fluid used was potassium bichromate 5 % 1 vol. + osmic acid 2 % 1 vol., the solution being made especially strong in osmic acid to allow for its subsequent dilution in the tissue. About 100 cc. were injected into each carotid, and, when the brain was opened an hour afterward, brown spots throughout the tissue showed where the fixation had begun. The result was that in places groups of cells lying close to large blood-vessels were impregnated, proving that the injection aided by infiltrating the tissue with larger quantities of bichromate thus securing the formation of more silver chromate in these places. Had the whole tissue been uniformly fixed in this way, which would have required a much larger quantity of fluid, the result would probably have been still better.

After the injection is completed and an hour or so allowed for fixation to take place, the brain is removed and suitable pieces placed in the hardening fluid. These pieces should

not exceed ½ cm. in thickness whether from an injected or from a fresh brain. This size is rendered necessary by the fact that the fixation by the hardening fluid extends inwards slowly, and because the diffusion of the silver cannot take place properly beyond a certain depth. This does not exclude the impregnation of large pieces, provided they are of the necessary thinness. Care must also be taken to cut the pieces to be impregnated as accurately as possible in the plane in which it is desired to section them subsequently; *e.g.* if it be desired to make sections displaying the whole length of the pyramid cells of the cortex, the cuts should be made perpendicular to the surface of the cortex; if the protoplasmic expansions of the cells of Purkinje, they should be made at right angles to the convolutions of the cerebellum, etc. If this precaution be not observed, much of the thin pieces impregnated will be wasted by cutting off corners with oblique cuts, etc. Furthermore, the impregnation is liable to vary at different depths from the cut surfaces of the piece, being especially full in details nearest the surface; hence it is obvious that sections passing parallel to these cut surfaces give better and more uniform fields.

The surface of impregnated pieces is usually covered with silver chromate, which mars the beauty of the preparations, and may also obscure details of structure lying near the surface. To avoid this, it has been recommended to cover the surface of the pieces, before hardening, with gelatine (Sehrwald) or with celloidin or blood (Cajal). Gelatine, however, interferes with the impregnation. Egg albumen might be adapted for this purpose, and should be smeared upon the surface (not necessarily upon the *cut* surfaces, however) either before or during the hardening.

The hardening fluid usually employed is potassium bichromate 3½% 4 vols. + osmic acid 1% 1 vol. Instead of this a mixture was sometimes used practically the same as that recommended by Berkley; *i.e.* osmic acid 2% 16 vols. + potassium bichromate 5% 84 vols. It is difficult to determine whether this be better than the ordinary mixture. Possibly its use results in the impregnation of a greater number of elements, owing to the fact that there is more bichromate of potassium in the tissue available for the formation of silver chromate.

Another requisite to success is that a sufficient quantity be used. It is not easy to give an absolute rule regulating the proportion between the amount of tissue and the quantity of fluid. The pieces may first be placed in a small quantity of the fluid. This soon becomes turbid, and after half an hour or an hour should be changed for a larger quantity of fresh fluid. This should be examined now and then, and if at any time it should be found to be turbid, or to have lost, or nearly lost, its characteristic smell of osmic acid (accompanied often by a darkening of the fluid), it should be changed for fresh fluid. As

an example, three pieces ½ cm. thick, and about 3 cm. by 4 cm., after being in a small quantity for an hour, were placed in a dish containing 100 cc. of the hardening fluid, which had to be renewed the next day. This probably represents the maximum quantity of tissue which could be hardened in such a quantity of fluid.

If the pieces have flat surfaces which lie quite closely applied to the bottom of the dish, a small quantity of absorbent cotton should first be placed in the dish, so that the hardening fluid may have easy access to all sides.

The crucial point in the method lies in the duration of hardening. How long the tissue shall be hardened depends upon (*a*) the kind of impregnation aimed at, (*b*) upon the kind of tissue, (*c*) upon the stage of development of the tissue, whether adult or embryonic, (*d*) upon the kind of animal, and (*e*) upon the temperature in which the hardening takes place.

(*a*) According to the rule laid down by Cajal for the cords of embryo chicks, and by Kölliker and Lenhossék for the human embryonic cord, the different elements are impregnated, according to the degree of hardening, in the following order: (1) Neuroglia (2–3 days), (2) Nerve cells (3–5 days), (3) Nerve fibres and collaterals (5–7 days). The times given apply to the human cord. This is only true in a very general way. Both neuroglia and nerve fibres usually appear in any preparations in which impregnation has taken place, irrespective of the duration of hardening. One factor of uncertainty, often overlooked, is caused by differences in the ratio between the bulk of tissue and quantity of hardening fluid. In proportion as the former is increased, the fluid becomes less efficient during the hardening, and thus a dish containing a certain quantity of tissue and hardening fluid may really be in a more advanced stage of hardening than a greater quantity of tissue placed in the same amount of hardening fluid for the same period of time.

If the tissue be underhardened, the result is often that it is filled, after impregnation, with a diffuse red precipitate of silver chromate. The effect of overhardening is usually a complete absence of any precipitate of any kind in the tissue or, possibly, the formation of numbers of clean, sharply defined black crystals. As the tissue progresses toward the maximum period of hardening, the tendency is for fewer elements, perhaps, to be impregnated, but those that are stained are brought out with greater cleanness. The tendency is also for the tissue to be more uniformly impregnated at all depths. This is probably due to the fact that the tissue is hardened more uniformly throughout when left in the hardening fluid longer.

(*b*) Respecting the kind of tissue, it is within the scope of the present work to deal with the central nervous system only, and no very definite rule can be laid down, owing to the factors just mentioned. I am inclined to believe that the cortex of the cerebellum requires

the briefest period of hardening, and that the cord possibly does not require quite the same length of time that the basal ganglia and cerebrum do.

(*c*) The stage of development of the tissue is an important element in the duration of hardening. In general, the older the tissue, the longer the period of hardening. Embryonic tissue is much more favourable than adult tissue. Good impregnations of nerve fibres cannot be looked for in tissue in which the fibres are medullated. It is not entirely true that the axis-cylinder of a medullated nerve fibre will never impregnate, but such fibres are decidedly unfavourable. In an eight-months human embryo, for example, many of the axis-cylinders of the pyramidal tracts, in some of the preparations, were apparently impregnated, while the medullated tracts of the cord and medulla had simply the faint brown stain due to the osmic acid used in hardening. This indicates that for the best study of the cord and medulla, younger material must be used than is necessary for the higher centres. The medullation of fibres is not the only cause of the difference between embryonic and adult tissue, however, for some cells impregnate better in embryonic tissue. This is possibly due to the different consistency of the embryonic tissue and also to the fact that its cells are smaller.

(*d*) The kind of animal used is another factor to be taken into account. Cajal has shown that in the mouse the elements of the cortex are very embryonic at birth, and that the most favourable age is from the 8th to the 25th day after birth. In larger mammals (*e.g.* the rabbit), he shows that this period is thrown back to between the 1st and 8th days after birth. This interesting tendency is still further exemplified in man; for, as the atlas shows, the cortical cells are well differentiated, though perhaps not in all respects completely developed, one and two months before birth. Consequently, also, the period of hardening would exceed that required for smaller mammals (with shorter gestation periods) of the same age relative to birth.

(*e*) A higher temperature naturally accelerates the hardening. The temperature of the room in which these impregnations took place rarely varied much from 21° C.

The best period of hardening in general for an eight-months human embryo, as can be seen from the table below, is six days, though good results in the cortex were obtained before this and also in tissue hardened eight days. Six days is also the best period for the medulla and basal ganglia. While cells may be obtained in the cortex before six days of hardening, six days is necessary to bring out the tangential fibres and Cajal cells. It is obvious, however, that it is best not to depend entirely upon any one period of hardening, but to transfer pieces at various intervals of time into the silver nitrate.

Impregnation. — After the hardening, the next step is to bring the tissue into the solution of silver nitrate. The solution used is a $\frac{3}{4}$ % in water, but a $\frac{5}{8}$ % or a 1 % solution may be

employed without producing any difference in the results. In other lines of work I have even used a 4 % and a 10 % solution, the effect apparently being to increase, sometimes, the number of elements impregnated with a tendency to lose, to some extent, cleanness of impregnation.

The pieces are brought immediately into the silver solution, and the first solution used may be one that has been used in a previous impregnation. The pieces are simply rinsed in this first solution, which need merely be sufficient to cover them. A copious precipitate is immediately formed, and then the fluid is poured off and thrown away. When a second quantity is poured upon the tissue, it usually clouds up slightly. This is again poured off, and the pieces are now brought into the final solution. This may again become discoloured, especially if the pieces be of some size, and should then be changed. The quantity of the solution in which the pieces finally rest should be considerable, even double the quantity of osmic-bichromate used in hardening. When brought into the final fluid, the pieces are placed upon absorbent cotton to facilitate the diffusion of the silver nitrate into the tissue.

The impregnation begins very soon. Golgi says it may begin immediately at the surface and be completed in favourable cases in 2–3 hours. It is generally completed in 12–24 hours. When the pieces cannot be cut at once they should be kept in the silver solution, and this should be changed whenever it shows a yellowish or greenish tinge. Tissues can be thus kept in silver for several weeks or even longer, though it is wise to cut them sooner.

Usually both hardening and impregnation are done in the dark. This is not necessary however. The light plays no part in the impregnation. When the pieces are to be kept in the silver for some time, it is better to keep them in the dark. At any stage in the procedure they may be brought into the light temporarily for examination, etc., without any fear of injury.

Besides the precipitation of silver chromate, and possibly of other silver compounds in the tissue, another change effected by the silver, to which I have not observed any allusion, is the clearing up of the blackening produced by the osmic acid in the hardening.

As above noted, one difficulty with the Golgi silver methods, is the slow and feeble penetration of the osmic-bichromate (in the rapid method), and also of the silver nitrate, so that impregnations are limited to a certain distance from the surfaces of the pieces besides being often more unequal than is desirable. The writer sought to overcome the latter and increase the diffusion of the silver by adding sulphates to the silver solution. The sulphates of sodium and zinc when thus added did not interfere with the impregnation, but whether they produced the desired effect to any extent is questionable. Their presence in some of the silver solutions given below need not be regarded as one of the requisites to obtaining the

impregnation. The manner in which the impregnation is facilitated when the tissue is placed in the silver by anything that stimulates diffusion, is shown in preparations by the fact that wherever a crack or a break in the piece exists, in that vicinity the greatest number of elements are impregnated. The addition of formic acid to the silver nitrate solution (one drop to 200 cc.) as recommended by Cajal, has not proved of any advantage.

Another modification of the silver solution may be mentioned here. It is at times desirable to double-stain preparations in order to bring out the unimpregnated elements. This may be done by a quick staining of the sections in any suitable dye dissolved in 95 % alcohol. Another method consists in adding the stain to the silver solution, the requirements being that the stain has a neutral reaction and does not affect nor is affected by the silver nitrate solution. Some of the anilines, *e.g.* acid fuchsin, and a neutral carmine solution, fulfil these requirements. This gives of course an *in toto* stain.

Cutting and Mounting. — Preparatory to cutting, the piece is transferred directly from the silver solution into 95 % alcohol. It may be left in this an hour, or longer, according to its size. The alcohol should be changed several times to free the tissue as far as possible from the silver nitrate. Pieces of tissue impregnated by the rapid Golgi method cannot be infiltrated with celloidin, as the prolonged immersion in alcohol, etc., is liable to injure the impregnation; nor, indeed, is it necessary, as sections can be readily cut of the desired thickness without imbedding. Consequently the piece is placed for a few minutes in a thin and then in a thick solution of celloidin, to give it support and to gum it upon the microtome block. After placing it upon the block, the celloidin is hardened by immersion in chloroform for a few minutes. This should not be too prolonged, or the tissue will crack or become friable.

The sections are cut in 95 % alcohol and kept in the same until cleared. They should be cut as a rule from 50 μ to 100 μ thick. Thinner sections cut the nerve cells and their processes into small pieces. Small sections can be removed from the knife with a brush; with larger ones, however, the slide must be brought up under the edge of the knife and the section gently washed or pulled down upon it. The upper surface of the knife should be as nearly level as possible, to avoid an accumulation of alcohol at the edge. If it be found impossible, on account of its size, to cut the unimbedded piece without considerable tearing, painting the surface of the block with a medium thick solution of celloidin must be resorted to. Not much time need be lost by this procedure, especially as sections are then more quickly removable from the knife. As the knife is pushed back over the block after a cut, the surface of the block is wiped dry by the knife, and the celloidin can then be applied to it with a brush. While the last section which has just been brought

upon the slide, if it be desired to mount them serially as described below, is being placed in position, the film of celloidin will dry sufficiently. Alcohol can then be applied and the next section cut.

For clearing, oleum origani cretici is preferred. It clears readily from 95 % alcohol, does not make the sections brittle, and sections may be kept in it for a considerable time, even a day or so, without injury. It is better before mounting to wash them briefly in xylol. The xylol allows the balsam to set more rapidly, and is less liable to affect the preparations than is the origanum brought over into the balsam with the section. On the other hand, xylol tends to make the sections crumpled and brittle.

In the handling and mounting, several methods may be employed. The sections may be brought from the origanum upon the slide, the oil blotted off, and a drop of balsam placed upon the section, the mount then being watched to see that the balsam does not run off. This has the disadvantage that a small quantity of origanum remains in the section, usually not enough to prevent the balsam from drying properly. Another mode of procedure is to bring the sections from origanum into xylol, and thence into a dish of balsam. The diffusion of balsam takes place while in this, and consequently when the section is lifted out and placed upon the slide, the balsam does not tend to run off. The disadvantage here is that sections of the central nervous system tend to become crumpled and brittle.

The best method, one which preserves the sections in serial order, and keeps them flat for photographing, is the following. The sections are brought from the knife and arranged on the slide in 95 % alcohol, and, after the slide is filled, the alcohol is blotted off and a thin solution of celloidin is quickly run over the slide and drained off. After the film has set by slightly drying, absolute alcohol is quickly run over the slide and drained off, thereby facilitating the subsequent clearing. Care must be taken not to dissolve the film. The slide is then immediately placed in origanum, where it may remain while the next slide is being filled. It is then placed successively in two dishes of xylol to remove the origanum. If the slide clouds up in xylol, it has not been completely dehydrated. Absolute alcohol may then be again run over the slide, which may then be again cleared in origanum. A slight opacity outside the sections will usually clear up after mounting. For the mounting medium a solution of damar in xylol is used.

The sections are mounted without a cover slip, and to do this properly is not as simple as would at first sight appear. The sections should be covered with a layer of balsam, which, when dry, should be even and as thin as possible and yet cover the sections. If a thin layer be applied at first, it runs off in spots, leaving the sections dry, and requiring constant watching, which interferes with other work. All this may be obviated by placing the slide,

after being brought from xylol, on a level table and flooding it with as much of a rather thick solution of damar as it will hold without overflowing. It can then be covered over so as to protect it from dust, and left at least half an hour and longer if convenient. Diffusion of the balsam into the celloidin and sections will then be completed, and the superfluous balsam may be drained back into the bottle. Just how much to leave on the slide depends upon the thickness of the balsam and must be determined by experience. After the superfluous balsam has been removed, the slides are put in an oven (50°-55° C.) over night to harden the balsam. One of the essentials to a good preservation of preparations, to avoid yellowing, etc., is that the balsam be quickly and completely hardened.

Besides the rapid method, certain of the preparations were made either by means of Golgi's mixed method or by means of what might be termed modifications of Golgi's long method, introduced by the writer.

Plates III., V., and VI. are taken from preparations made by means of Golgi's mixed method. Here the cord was placed in Müller's fluid (potassium bichromate alone answers as well) for one week, then for several days in osmic-bichromate, and finally in silver nitrate. This method was not used very extensively. It appears to be especially adapted to bringing out the cells rather than the fine plexus of fibres, and is particularly applicable to adult tissue. Cajal recommends it especially for the demonstration of the cells and transverse fibres of the molecular layer of the cerebellum in young mammalia. It was the method most strongly recommended by Golgi himself. This method, furthermore, permits the tissue to be kept, as Golgi points out, for from two to thirty days in bichromate, from which, at convenient times, pieces can be removed and placed into osmic-bichromate and thence into silver nitrate. Whether this could equal the rapid method with embryonic material has perhaps been hardly sufficiently tested, but the quick fixation of the rapid method would appear to be especially desirable with the more delicate and less firm embryonic tissue.

The long Golgi method has not been employed in preparations shown in this Atlas. The impregnations made by the long method differ from those made by the rapid method in the fact that they possess greater stability in strong alcohol, in which they may remain for a considerable period without deterioration. The method is especially indicated for the adult cerebrum and cerebellum, but one of the two modifications given below is probably easier.

It has been found by the writer that lithium bichromate hardens tissue much more rapidly than the potassium salt, and, by employing the former, the period of hardening may be cut down to a few days.

Since the introduction of formalin for hardening, Hoyer, Jr., discovered that material kept in it could be afterwards impregnated like fresh material, and that the osmic acid could in

this case be dispensed with. The writer found subsequently, but independently, that fresh tissue could be placed immediately in a mixture of formalin and potassium bichromate, and thence brought into the silver nitrate solution. Thus formalin may be substituted for osmic acid, but it has to be used in much larger proportion.[1]

The best proportions for the fluid and periods of hardening for this method have not yet been sufficiently worked out. The addition of from $2\frac{1}{2}$ % to 30 % of formalin to $3\frac{1}{2}$ % to 5 % of bichromate, and a period of hardening for 18 hours or upwards, have all been recommended. In fact, considerable latitude in both respects appears to be allowable. The results are similar to those of the long Golgi method, which it also resembles in the fact that pieces of impregnated tissue, or sections therefrom, can be left in strong alcohol for a considerable period, days or even weeks, without deterioration. It is not improbable that this will prove the best method, when properly developed, for the adult central nervous system of mammals, but it is not as well suited for embryonic tissue as the rapid method of Golgi. Its defect lies in its deficient hardening power. With adult tissue, where the osmic-bichromate mixture penetrates very poorly, and also overhardens the periphery, this defect is an advantage. Another advantage of this method is, that the favourable period for impregnation is not, apparently, passed through so rapidly in the hardening. If brains are injected through the carotid arteries with a solution strong in formalin (*e.g.* formalin 1 vol. + potassium bichromate 10 % sol. 1 vol.), the best results of both hardening and subsequent impregnation may be obtained.

The following table will give further details as to how the majority of the preparations here reproduced were made. By "used" is meant a solution which had been previously used but remained in good condition. As a rule, it is better, however, to use a fresh solution. By "osmic-bichromate" is meant a solution consisting of potassium bichromate $3\frac{1}{2}$ % 4 vols. + osmic acid 1 % 1 vol.

PLATE.	HARDENING FLUID; TIME OF HARDENING.	SILVER SOLUTION.
III., V., & VI.	Müller 1 wk., osmic-bichromate several days	Silver nitrate $\frac{3}{4}$%
VII., VIII., IX., & X.	} Berkley's solution (used) 2 da. 20 hrs.	{ Zinc sulphate 2% 1 vol. } 100 cc. + 2 drops { Silver nitrate 2% 1 vol. } formic acid.

[1] The substitution of formalin for osmic acid in the hardening was first made by the writer during the summer of 1894, and the fact announced in a note to his article "The Cranial Nerves of Amphibia," dated July, 1894, which appeared in the "Journal of Morphology," Vol. X. No. 1, January, 1895. A communication was read before the New York Academy of Sciences Jan. 14, 1895, an abstract of which appeared in the "Anatomischer Anzeiger" for March 15, 1895 (Bd. X. No. 15). In the number for June 13, Durig records similar observations, the March number of the "Anzeiger" not having come into his hands when his communication was sent off. In the number for July 19, Lachi calls attention to the fact that this mixture was recommended by him in the "Monitore Zoologico," 1895, Anno. VI. No. 1, and also by Isola in the "Bullettino della R. Accademia Medica di Genoa," 1895, No. 2, and in the "Gazzetta degli Ospedali," February, 1895.

PLATE.	HARDENING FLUID; TIME OF HARDENING.	SILVER SOLUTION.
XI.	Berkley (used) 2 hrs., osmic-bichromate 50 hrs.	{ Silver nitrate 2% 1 vol. } { Sodium sulphate 2% 1 vol. }
XII.	Osmic-bichromate + 2½% of formalin (unnecessary) 18 hrs.	Silver nitrate 1%
XIII.	Osmic-bichromate (used) 4 da. 15 hrs.	Silver nitrate ½%
XV. & XVI.	Lithium bichromate 2½% 3 da. 3 hrs.	Silver nitrate 1%
XVII. & XVIII.	Potassium bichromate 5% + 5% of formalin, 22 hrs.	Silver nitrate 1%
XX., XXII. to XXXII., inc.	Osmic-bichromate 6¼ da.	Silver nitrate ⅚%
XXI.	Osmic-bichromate 2 da.	Silver nitrate ¾%
XXXIII., XLII. to XLIV., inc.	Osmic-bichromate 5 hrs., Berkley's solution 6 da.	Silver nitrate ¾%
XXXV. & XXXVI.	Osmic-bichromate 5 hrs., Berkley's solution 6 da.	{ Silver nitrate 2% 1 vol. } 200 cc. + 2 drops { Zinc sulphate 2% 1 vol. } formic acid.
XXXVIII.	Osmic-bichromate 2 hrs., Berkley's solution 2¾ da.	Silver nitrate ¾%
XXXIX., XLV. to XLVIII., inc., L.	Osmic-bichromate 7 da. 20 hrs.	Silver nitrate ⅚%
XLI.	Osmic-bichromate 2¾ da.	{ Silver nitrate 4% 1 vol. } { Zinc sulphate 10% 1 vol. }
LI.	Osmic-bichromate 6 da. 4 hrs.	{ Silver nitrate 2% 1 vol. } 200 cc. + 3 drops { Zinc sulphate 2% 1 vol. } formic acid.

The Golgi method, like all special methods, has its peculiar defects, which are liable to lead to misinterpretation. If, however, familiarity be acquired with the various appearances it gives, the careful investigator will not be misled by irregular precipitations, etc., any more than he is in other directions when using other special methods. Its great value in the investigation of nervous histology cannot but be admitted by all.

THE PHOTOGRAPHIC TECHNIQUE

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In photomicrography it is essential that the optical parts of the apparatus used, termed the system, should have their centres in the same straight line, and that this system, together with the camera, should be so mounted as to be as rigid and free from vibrations or accidental displacement as possible. These conditions were fulfilled by the apparatus used, which was the large photomicrographic outfit of Carl Zeiss of Jena, in the laboratories of the College of Physicians and Surgeons.

This consists of two heavy iron stands, upon one of which rests the camera, supported by wheels, so that it can be rolled backward and forward without being displaced laterally; thus the operator is enabled to observe the object directly through the microscope without altering the centring of any of the parts of the system. The second stand supports a broad table, upon which is the microscope, inclined to the horizontal position, and an optical bench of two parallel metal rails, upon which are fastened by set screws the accessory parts of the system. These vary with the work, but are usually coloured light filters for altering the white light to a monochromatic light, or screens for otherwise modifying it, diaphragms for centring and for limiting the size of the light pencil, condensers, and reflecting mirror. The electric arc used was so made as to fit the optical bench and be mechanically centred both laterally and vertically. The weight of the two stands insured rigidity, and the mechanical adjustments of the different parts were easily made, so that a beam of light from the electric arc or from the heliostat would pass through the optical centres of the system of lenses and be projected upon the centre of the ground glass screen of the camera. Where possible, sunlight reflected from the speculum of an heliostat was the illuminant, and was used in preference to other sources of illumination; but, as in these latitudes during the winter season there are many dark and cloudy days, it was found necessary to resort frequently to the electric arc, which, as recently improved, gave results that left little to be desired.

It would seem at first, as the Golgi stain is a metallic impregnation and opaque, that the use of isochromatic plates and a colour screen would have been unnecessary, but those

familiar with the Golgi preparations know that the tissue surrounding the silver impregnated cells and processes frequently has a decidedly yellow colour, which more or less rapidly darkens, and as it was desired to reproduce the effect of the cells and their processes upon a nearly or quite colourless background, it was found advisable to use both colour-sensitive plates and an orange-yellow screen. In previous work it had been the custom to use as a colour screen a glass cell containing a solution of one of the Tropæolins. The use of such a cell is not, however, unattended with difficulties; it is somewhat troublesome to make up anew each time, as so doing involves the use of the spectroscope if accuracy be desired; it is subject to change from dust, from evaporation, and in a short time from precipitation of the dye from its aqueous solution. In lieu of the glass cell, therefore, an unexposed lantern slide plate was fixed in sodium thiosulphite and well washed; when dry it was placed upon a level surface, gelatine-coated side upwards; upon this was poured a strong solution of Tropæolin in alcohol, which was allowed to evaporate protected from dust; Canada balsam was then poured over the dyed plate and a cover glass applied. The plate thus prepared was allowed to harden under pressure in a vertical position. A darker coloured screen was made by putting two dyed plates face to face in the same manner. The screens so made have proved very convenient, show scarcely perceptible fading or change during two years of constant use, and do away entirely with all the trouble incident to glass troughs and fluids.

The optical apparatus consisted of a Zeiss' Abbe condenser specially made for photography of 1 N. A. and achromatic, and of the following objectives: a Zeiss 2 mm., 3 mm., 4 mm., 8 mm., and 16 mm. apochromatic lenses, a 35 mm. projection lens of Zeiss, a $\frac{1}{4}$-in. Bausch and Lomb, a 1-inch Ladd of London, and a 3-inch Ross of London. No eyepiece was employed with the dry objectives, the camera length being 140 cm., which gave a magnification of from 25 to 190 diameters; with the oil immersion apochromats 2 and 3 mm. a projection ocular No. 4 was used and a camera length that gave from 1000 to 500 diameters by stage micrometer measurement. It was found when the image was thrown upon the screen that no matter how carefully the light was centred there would remain diffraction spectra, and the phenomenon known as halation manifested itself in this peculiar way, the stain being an impregnation of the chromate of silver and absolutely opaque, the light would be refracted around the edges of the cell bodies and large processes, and would appear on what should have been a perfectly black image as little tufts and jets of white (plates Nos. XIV. and XXXIV. are examples of this being among the first taken). In order to obviate both these difficulties a plate of finely ground glass was inserted, with its plane at right angles to the optical axis of the system, between the condenser and source of light, and placed so as to be within the focus of the condenser when both condenser and objective were focussed upon the
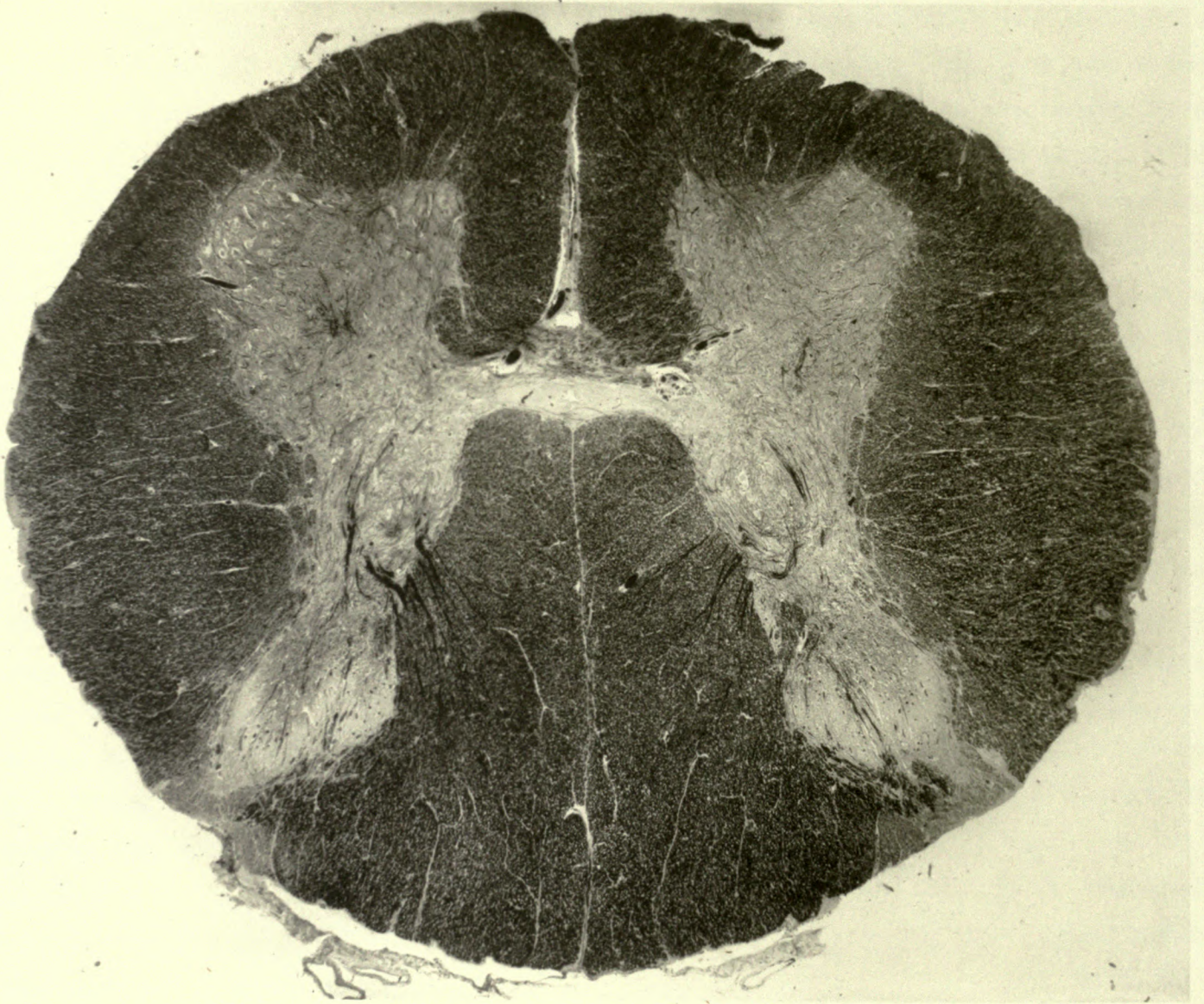
object; this gave a softly, evenly illuminated field, particularly free from the defects mentioned above, and with the sources of illumination used — the sun and the electric arc — the prolongation of the exposure was not sufficient to cause inconvenience from casual vibrations. All development was carried on with a single solution hydrokinon developer, composed of hydrokinon, 5 gr., sulphite of soda 20 gr., carbonate of potash 15 gr., to the ounce of water. When fully developed the plates were fixed in a solution of sodium thiosulphite, rinsed thoroughly and placed in a saturated solution of alum for five or ten minutes, washed in running water from one to two hours and allowed to dry spontaneously. The plates were not retouched in any manner, as it was most desirable that the finished prints should be entirely photographic and should be as little affected by the personal equation of the operator as possible; it was for this reason also that the artotype process of Mr. Bierstadt was chosen for the reproductions. This is the well-known gelatine process which is used under various names in this country and in Europe, and may be briefly described as follows : The negative is placed in contact with a glass plate coated with gelatine containing bichromate of potash (bichromated gelatine) and then exposed to light, as in ordinary photographic printing. Gelatine is hygroscopic and unaffected by light, but bichromated gelatine is rendered insoluble and incapable of absorbing moisture by the action of light in direct proportion to the length of time the light action continues. The light passing through the transparent portions of the negative renders the bichromated gelatine beneath non-absorbent, the partially opaque parts of the negative allow a varying light action according to the degree of density of the silver deposit, and the opaque parts prevent any action of light on the bichromated film ; as a result, therefore, the negative is reproduced in all its details of light and shadow by the varying power of absorption of the bichromated gelatine. The action of the light having continued for the proper length of time, the plate is removed from beneath the negative and placed in cold water, in the dark, until all the bichromate of potash has been dissolved out; it is then allowed to dry and is ready for the press. The plate is then firmly fixed in a horizontal position in a common lithographic printing-press, with the gelatine coating uppermost, and saturated with water, which is absorbed by the gelatine, as stated above, in a degree varying inversely as has been the amount of action of the light; the surplus water is then removed and a roller charged with printer's ink is rolled over it in all directions. The ink used is a greasy ink and will adhere to the non-absorbent portions of the plate, but will be repelled by the moist portions either wholly or partially, according to the amount of moisture they retain. When sufficiently inked, a sheet of paper is laid upon the plate and receives the pressure, as in ordinary printing, the ink is transferred from the plate to the paper, and the result is a finished print.

HUMAN SPINAL CORD; SECOND DORSAL SEGMENT.   WEIGERT STAIN.   X 25 DIAM.

PLATE I.

THE SPINAL CORD

THE general appearance of a transverse section through the human adult spinal cord is shown in Plate I. The level is at the upper part of the lumbar enlargement. This section was stained by the Weigert hæmatoxylin method. The diagram (Fig. 1) will assist in the explanation of its chief features, and the details of structure are shown in Plates II. to XI.

The H-shaped arrangement of the gray matter of the cord, and the fact that the gray matter is everywhere surrounded by white columns, which are darkly stained, is clearly marked. It is evident that the anterior horns form the larger part of the gray matter; that their contour is irregular, owing to the massing of cells into groups, which cause a projection of the gray into the white matter; and that they do not reach the surface of the cord. In the diagram three cells (*a*) are shown representing three groups of anterior horn cells. These cells are motor in function, presiding over the reflex movement and nutrition of the muscles, each group representing a single muscle, or a group of muscles whose action is conjoined. Many fibres are seen in the plate to issue from the anterior horns of the cord and to pass through the anterior column to the surface. These are the anterior nerve roots. Their course is shown in the diagram. In their course while in the gray matter they give off fine branches which end about other cells in the vicinity.

The posterior horns of the cord are smaller than the anterior horns; they nearly reach the surface of the cord and present a club-shaped appearance at their extremities where the substance of Rolando is situated. The cells of these horns are too small to appear in the plate, but are shown in the diagram. It will be noticed that two of these cells (*b*) send their neuraxons into adjacent columns of white matter, while a third (*c*) is confined to the posterior horn itself. At the base of each posterior horn, on its median side, a group of cells is to be seen in the plate; this is the Clarke column of cells. It is indicated in the diagram by a single cell (*d*) whose neuraxon is seen to pass outward to the periphery of the cord where it turns upward in the direct cerebellar column.

In the gray matter of the cord, scattered irregularly through it, between and within the anterior and posterior horns, there lie many cells whose existence is better shown in Plate II.

These are indicated in the diagram. Their neuraxons pass out into the adjacent white columns of the cord, where they bifurcate, one division turning upward, the other downward. These neurons have as their function to associate the action of various segments or levels of the cord. They are termed Strangzellen by German writers, who classify and name them according to the column into which their neuraxon passes. They may be called the intrinsic cells of the cord. Lenhossék[1] affirms that some of these cells appear to send out a neuraxon which divides into two parts, each of which goes to a separate column. In the diagram it will be seen that these intrinsic cells (e) send neuraxons into all the various columns. One set of these cells should be especially noticed, which send their neuraxons upward in the periphery

FIG. 1.

FIG. 1.—Diagram of a transverse section of the spinal cord.

On the right side the columns of the cord are shown and the fibres entering the gray matter from these columns. *I*, anterior median column. *II*, antero-lateral column. *III*, lateral limiting layer. *IV*, ascending antero-lateral tract of Gowers. *V*, direct cerebellar column. *VI*, pyramidal column. *VII*, Lissauer's column. *VIII*, column of Burdach. *IX*, column of Goll.

The posterior nerve roots are shown on the right side of the diagram and their various methods of termination in the gray matter. *1*, fibre entering Lissauer's tract. *2*, fibre entering posterior horn. *3*, fibre entering posterior horn and terminating deep within it. *4*, fibre entering column of Burdach. *5*, fibre passing to root zone of column of Burdach and sending the collateral fibre to the anterior horn. *6*, fibre entering root zone and sending collateral to the Clarke column of cells. *7*, fibre entering root zone and passing by way of the gray commissure to the opposite side of the cord. *8*, fibre entering posterior horn through root zone having come up from a lower level.

On the left side the various cells of the gray matter are shown. *a*, motor cells with motor nerve roots passing out of the cord. *b*, intrinsic cells of the posterior horns: one lies on the margin, is a "border cell"; the other lies deep within the horn, they send neuraxons into the posterior and lateral columns respectively. *c*, intrinsic cell of the posterior horn; Golgi's second type. *d*, cell of the column of Clarke with its neuraxon passing outward to the direct cerebellar column. *e*, intrinsic cells of the anterior and median gray with their neuraxons passing into the antero-lateral column. *f*, intrinsic cell in median gray sending its neuraxon to the ascending tract of Gowers. *g*, commissural cells in the median gray sending their neuraxons to the other side of the cord. *h*, sensory cell sending neuraxon to opposite column of Gowers.

[1] Lenhossék, Der feinere Bau des Nervensystems. 1895.

of the antero-lateral column in the division of it known as Gowers' tract (*h*). These are supposed to be sensory in function and to transmit sensations of pain and temperature. There are other cells in this median region of the gray matter which send their neuraxons across the median line through one of the commissures to the opposite side of the cord (*g*). These are known as commissural cells, and serve to transmit sensory impulses across the cord. Many of the cells of this median gray matter are concerned in the reception and transmission of sensations received through the posterior nerve roots.

The gray commissure uniting the two halves of the gray matter of the cord has in its centre the central canal. This is seen in Plate II. to be lined with cylindrical epithelium. The white commissure lies in front of the gray and contains many decussating fibres.

The entrance of the posterior nerve roots is well shown in Plate I. The nerve fibres enter the cord at the apex of the posterior horn; some pass directly into the horn, traversing the substance of Rolando, but the majority enter the horn from its median surface, passing through what is known as the root zone of the posterior column on the way. Some of these fibres are seen to end in the gray matter near the column of Clarke. Others may be traced toward the anterior horn. The actual direction and destination of these posterior roots are shown in the figure (see also Fig. 2, p. 18, and Fig. 3, p. 24). The anterior fissure of the cord containing blood-vessels, and the posterior septum, are also shown in the plate.

The white matter is made up of longitudinal fibres whose cut ends appear in the plate as fine round white dots. In a normal cord thus stained there is no evident distinction between the various columns of the white matter, though a posterior, lateral, and anterior portion can easily be made out. The various columns as determined by pathological investigation are as follows, and their situation is shown in Figs. 1 and 2.

I. Anterior median column contains fibres from the motor cortex of the hemisphere which have come through the pyramid of the medulla and have descended without decussating. These fibres pass into the anterior gray matter and terminate in a fine brush-like expansion about the cells of the anterior horn. They transmit impulses of voluntary motion.

II. Antero-lateral column surrounding the anterior horn of the cord contains fibres passing in both directions, which arise from cells lying in the anterior horn. These fibres pass from the cells into the column, then bifurcate, turning both upward and downward, pass a long or short distance through the column, giving off collateral branches in their course, then reënter the anterior gray matter, and terminate, as do also the collaterals, in brush-like expansions about the cells of the anterior horn. They transmit impulses of association which harmonize the action of motor cells at various levels. This column is traversed by the anterior nerve roots.
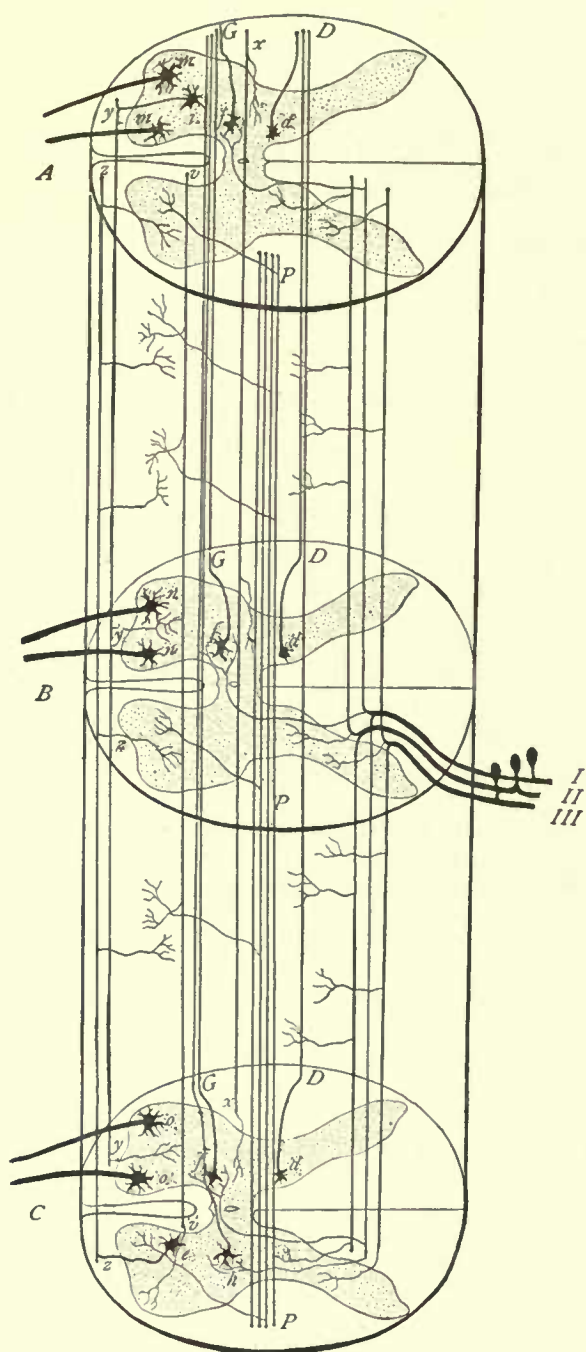
c

FIG. 2.

FIG. 2. — Diagram to illustrate the transmission of sensory, motor, and association impulses through the spinal cord.

III. Lateral limiting layer, a layer of white fibres adjacent to the median and posterior gray matter, contains short fibres of association, whose origin is from cells in the median portion of gray matter and whose course is similar to those in II. Their termination is about the cells of the same region at different levels. This layer is traversed by many fibres from the other lateral columns, entering and leaving the gray matter.

IV. Ascending antero-lateral tract, or column of Gowers, lying on the surface of the cord, contains fibres whose origin is in cells situated in the median gray matter. These fibres traverse the other columns and turn upward in this column, passing into the antero-lateral field of the medulla and through the formatio-reticularis of the pons into the internal capsule. They transmit sensations of pain and temperature upward to the brain from the cord. Among these fibres in this column are also descending fibres which come downward probably from the cerebellar hemisphere, but do not form a separate column.

V. Direct cerebellar column, lying on the surface of the cord behind the last named column, contains fibres which arise from the cells of the column of Clarke, and after traversing the other lateral columns, turn upward in this column, and pass to the cortex of the cerebellar hemisphere. They transmit sensations of equilibrium. (See also Fig. 7, p. 42.)

A, B, C, are three levels of the cord. *I, II, III,* are sensory nerve roots entering the posterior root zone at level, *B,* bifurcating, ascending and descending, and sending collaterals into the gray matter at many levels. Three such collaterals are shown at *A, B, C,* ending in the posterior horn, and opposite median gray. The collaterals shown in diagrams 1 and 3 are not shown here. The collateral which crosses to the opposite side terminates about the cell, *f,* which sends its neuraxon into the column of Gowers, *G,* and thence upward to the medulla. At level *C* a collateral ends about sensory cell, *h,* which sends its neuraxon also into *G.* The collateral entering the base of the posterior horn terminates about the column of Clarke on the same side. For the sake of distinctness the cell, *d,* of the column of Clarke is shown on the opposite side with its fibre entering the direct cerebellar column, *D,* and ascending to the cerebellum. *x,* descending cerebellar tract sending its collateral fibres into the median gray. *e,* intrinsic cell of the anterior horn at level, *C,* sending its neuraxon into the antero-lateral column, *z,* where it ascends, giving off collaterals, *z,* at levels *B* and *A,* and proceeding upward to the medulla. *i,* intrinsic cell at level, *A,* sending its neuraxon into the antero-lateral column, *y,* where it ascends and descends, sending its collaterals, *y, y,* into the anterior horns of levels *B, C.* *P,* pyramidal tract giving off collaterals which pass to the anterior horn of the cord and terminate in brushes about the motor cells. The motor cells, *m, n, o,* are shown for the sake of distinctness on the opposite side. *v,* anterior median column with collateral entering the anterior horn and terminating in brushes around the motor cells.

VI. Lateral pyramidal tract contains fibres from the motor cortex of the opposite hemisphere which have come through the pyramid of the medulla and have decussated in the medulla. These fibres descend and give off many collaterals, which, like their terminals, turn inward and forward and terminate in a plexus of fine fibrils about the cells of the anterior horn. They transmit voluntary motor impulses.

VII. Lissauer's column is a small collection of white fibres of short course derived from the posterior nerve root, which lies on the apex of the posterior horn. These fibres bifurcate on entering the column and pass up and down for a short distance, finally entering the posterior horn, to which they give also many collaterals. The fibres terminate in brush-like expansions about the cells of the posterior horn.

VIII. The column of Burdach consists of three divisions: (1) the root zone near the posterior horn, through which pass many of the posterior root fibres which bifurcate on entering the zone and turn up and down, giving off numerous collaterals which enter the posterior horn through the root zone; (2) the median portion of the column which contains long fibres passing from the posterior nerve root up to the cuneate nucleus of the medulla; (3) a peripheral zone containing other long fibres passing chiefly upward, but finally turning inward to the posterior horn. Mingled among these three divisions are many association fibres whose origin, termination, and collateral destination are in the posterior horns. These fibres are all sensory in their function.

IX. The column of Goll consists wholly of long fibres which have entered the cord in the posterior nerve roots of the sacral, lumbar, and lower dorsal regions and pass upward to the nucleus gracilis of the medulla. They transmit sensory impulses.

The constituents of the posterior nerve root require to be mentioned, a number of different destinations being shown in the figures. These root fibres all bifurcate on entering the cord, their divisions turning upward and downward. The downward division is short, and soon turns into the gray matter, terminating in a brush-like expansion either in the posterior or median gray matter about the intrinsic cells of the cord. The upward division is long, and passes a varying distance toward the medulla, some fibres extending up the entire length of the cord. Both divisions give off numerous collaterals which terminate like their true ends. Some collaterals pass directly into the posterior gray horn and end there; others pass to the Clarke column of cells; others pass by way of the posterior commissure to the other half of the cord to terminate in the median gray matter; others pass directly through the median gray to the anterior horns ending near the motor cells. These last are the paths of reflex action. Impulses entering the cord thus are transmitted to the vicinity of the intrinsic cells of the cord, which then take them up and send them on to the brain by various tracts lying in the different columns already described.

Plate II. shows a transverse section through a human fœtal cord at the eighth month stained by the Golgi method. The ratio of the white to the gray matter is very small at this period of development. The cells of the gray matter are, however, already formed, and their processes are well developed, but their separation into groups is not yet very manifest. It will be noticed that the cells are irregularly scattered throughout the anterior horn and the central gray matter, and extend back into the posterior horns to some extent. It will be noticed that the cells are large in comparison with the size of the cord; that they have very numerous branches which pass in all directions, forming an interlacing mass of fibres which touch but do not unite. In the commissures of the cord it will be noticed that there are many of these fibres crossing from one side to the other. The substance of Rolando is seen to be devoid of cells. The various cells of the cord may be classified as follows:

I. Root cells, lying in the anterior horn or median portion of the gray matter, whose neuraxons pass out of the cord chiefly through the anterior nerve roots, but also in part through the posterior nerve roots.

II. Intrinsic or columnar cells, lying in all parts of the gray matter, whose neuraxons do not leave the cord, but pass into the columns, bifurcate, and after traversing some extent of the cord reënter the gray matter and end. Several varieties of these cells are described according to the destination of their neuraxons. (*a*) Cells of a single column; the neuraxon passing into one column only. (*b*) Cells of two columns; the neuraxon dividing, one branch going to one column, the other to another. (*c*) Commissural cells; the neuraxon crosses the middle line and ends in the gray matter, or turns up or down in a column, finally entering the gray matter again. (*d*) Cells which are both commissural and columnar; the neuraxon divides and one part crosses while the other enters a column on the side of the cell.

III. Cells of Golgi's second type;[1] the neuraxon divides and subdivides in the gray matter and does not leave it to enter the roots or columns.

[1] C. Golgi, Sulla fina anatomia degli organi centrali del sistema nervoso. Milano, 1885. Untersuchungen über d. feinere Bau d. Nervensystems. Atlas u. Text. Jena, 1894.

HUMAN SPINAL CORD OF EMBRYO EIGHT MONTHS. GOLGI STAIN, SHOWING CELLS WITH
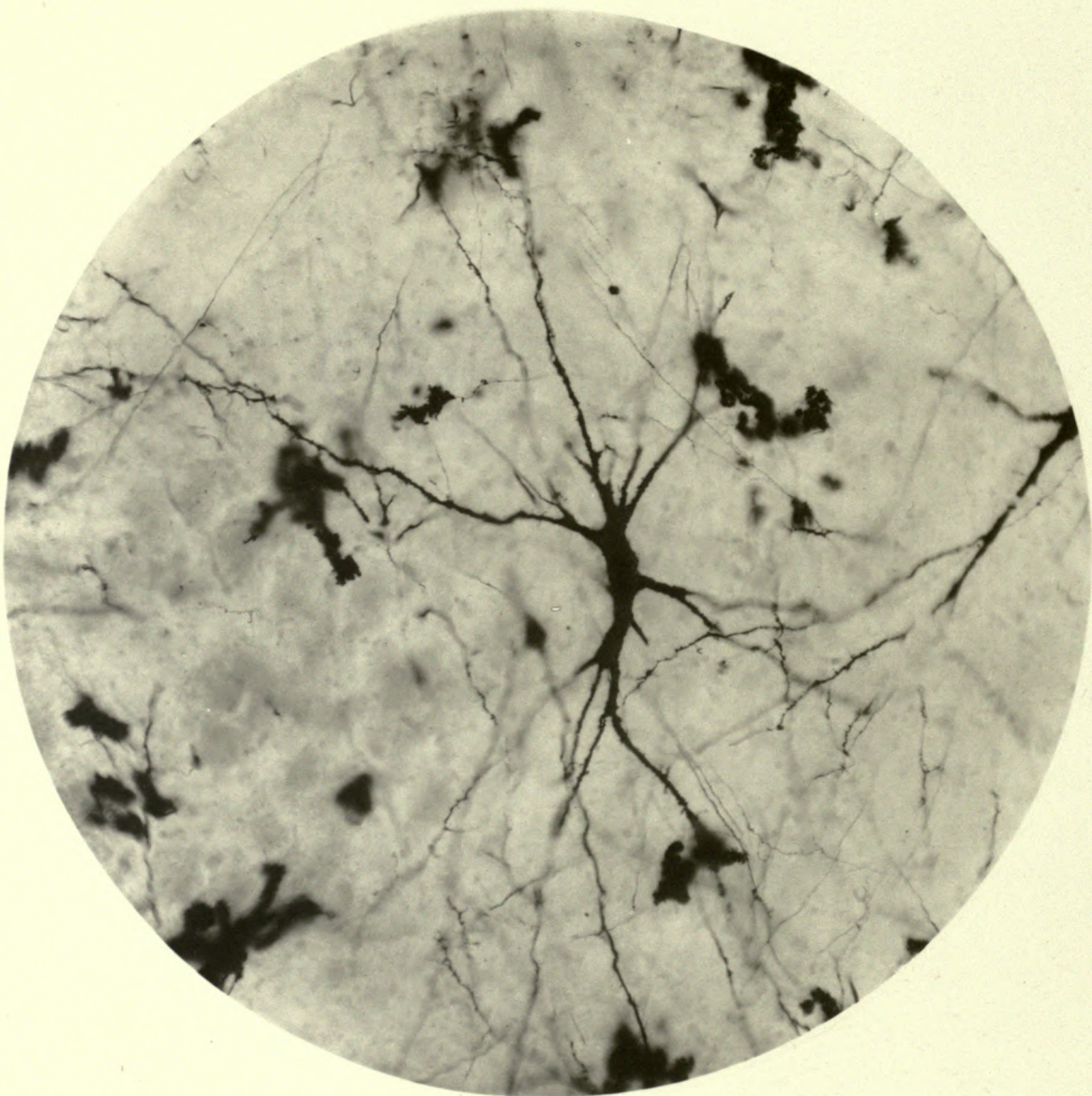BRANCHES. X 45 DIAM.

PLATE II.

LARGE CELL OF THE ANTERIOR HORN OF THE SPINAL CORD OF A FOETAL PIG, SHOWING
NUMEROUS DENDRITES, AND THE NEURAXON ISSUING FROM THE LOWER END OF THE CELL, AND
GIVING OFF A COLLATERAL AT A RIGHT ANGLE IN ITS COURSE.   X 190 DIAMETERS.

PLATE III.

Plates III. to VIII. show the large cells of the gray matter of the spinal cord both in transverse and in longitudinal section. These cells are of various shapes with numerous branches. They measure from 70 to 130 μ. There are long narrow cells whose branches have two principal directions, as shown in Plate III. There are oval or polygonal cells with branches running in many directions, as shown in Plates IV. to VIII. In all these cells it is possible to distinguish a large body, which by other methods of staining can be shown to contain a nucleus and nucleolus, and two varieties of branches characteristic of all nerve cells; viz.: dendrites and neuraxons.

THE DENDRITES are branches which come off from projections of the body of the cell. They are thick near the cell, but diminish in size as they pass outward. They present numerous offshoots in their course, branching like the limbs of a tree. The size of the dendrite varies in its course, and it may present a varicose appearance. The surface of the dendrite is not smooth, but presents a fine moss-like or furry appearance. The dendrites and their branches terminate in free ends which usually have a little knob-like swelling upon them. Some of the dendrites are very long. Others are quite short and terminate near to the cell. The dendrites are made up of protoplasm similar to the cell body, and hence were formerly called protoplasmic processes. It has been thought by almost all authorities (Ramon y Cajal,[1] Van Gehuchten,[2] Lenhossék) that they collect the impulses going to the cell, from the fine neuraxons of other cells, whose terminals reach the gray matter, and hence are cellulipetal in function. This is the view generally accepted. It has been thought by Golgi that they have a purely nutritive function and play no part in the action of the cell, being in relation with the blood-vessels at their extremities and thus collecting nutrient substances for the cell, just as the roots of a tree nourish its trunk. This view has, however, not met with any general acceptance, for Lenhossék has shown that the dendrites develop long before the blood-vessels, and do not depend upon these latter for their direction or distribution. It was formerly believed that after many branchings the dendrites of one cell united with those of other cells, forming thus a network of fine fibres throughout the gray matter (Gerlach). Golgi refuted this theory, and it is now known that no such network exists; and that while the dendrites may interlace and probably touch one another, as do the adjacent leaves and branches of the trees in a forest, they never really join one another, and are thus as independent of each other as are the trees. Thus each nerve cell with its dendrites must be considered as a separate entity.

The cells, however, are in a close functional relation with one another though not joined

[1] S. R. Cayal, Les Nouvelles Idées sur la Structure du Système Nerveux. Paris, 1894. Also Internationale Monatschrift f. Anat. u. Phys. Bd. VI., VII., VIII., and La Cellule, Tome VII. and IX.

[2] Van Gehuchten, Le Système Nerveux de l'Homme. Lierre, 1893.

together, and it is supposed that an activity in one may excite activity in others, through the medium of neuraxons and dendrites either by accidental contact, or, more probably, by the induction of impulses in the one from the other; just as an electric current in one wire will set up a current in independent wires about it.

Plate IV. shows a large motor cell of the anterior horn of the spinal cord of a fœtal pig, with numerous dendrites. The interlacing of the dendrites is particularly evident in the plate, where many dendrites belonging to cells not shown in the plate intertwine with those whose origin is shown. Gerlach believed that the sensory nerve fibres after entering the cord became continuous with the ends of the dendrites, and that thus sensory impulses are sent into nerve cells. But this theory has been abandoned, and the free termination of all dendrites must be accepted. There is no continuity between nerve fibres and dendrites. There is no real network of nerve fibres in the nervous system. The sensory impulses come in, as we shall soon see, by nerve fibres which terminate in free ends like brushes, and their brush-like expansions may surround the nerve cells or may interlace with their dendrites, but do not necessarily come into contact with them. In Plate V. just below the cell such a free termination is to be seen, there being little knobs on each terminal filament.

THE NEURAXON is the second variety of branching process of the nerve cell. It was formerly known as the axis cylinder projection or the functional process of the cell. The neuraxon may come off directly from the body of the cell or from a small pyramidal projection of the body as in Plate IV., or it may arise from one of the large dendrites near the cell body. The characteristics of the neuraxon which serve to distinguish it from the dendrites are its uniform size from its origin onward, the possession of a myelin sheath giving it a smooth surface, and its lack of many branches. It was formerly supposed that the axis cylinder process never branched. This, however, is not so. The neuraxon gives off branches called collaterals, but these differ greatly from the branches of the dendrites. In the first place, the branches of the neuraxon are usually given off at right angles to its direction; in the second place, they are always very small and fine as compared with the neuraxon. There is often a slight swelling of the neuraxon at the point of origin of a collateral, as may be seen in Plates IV. and VI. In Plates III. to VIII. numerous neuraxons can be seen with fine collaterals coming off from them. They are seen to interlace with the dendrites, but their smaller size, regular smooth contour, and method of giving off branches, nearly at right angles, serve to distinguish them from dendrites. Golgi considers that it is only through the neuraxon that the cell performs its function, but this, as already stated, is not accepted. Van Gehuchten and others have agreed that all neuraxons are cellulifugal in function, conveying impulses outward from the cell, but this too is not fully established.

LARGE CELL OF THE SPINAL CORD OF A FOETAL PIG, SHOWING NUMEROUS DENDRITES WITH
BRANCHES, AND THE NEURAXON WHICH PROJECTS UPWARD. INTERLACING NEURAXONS OF OTHER
CELLS WITH COLLATERALS ARE SEEN BELOW THE CELL, AND MANY DENDRITIC BRANCHES OF OTHER
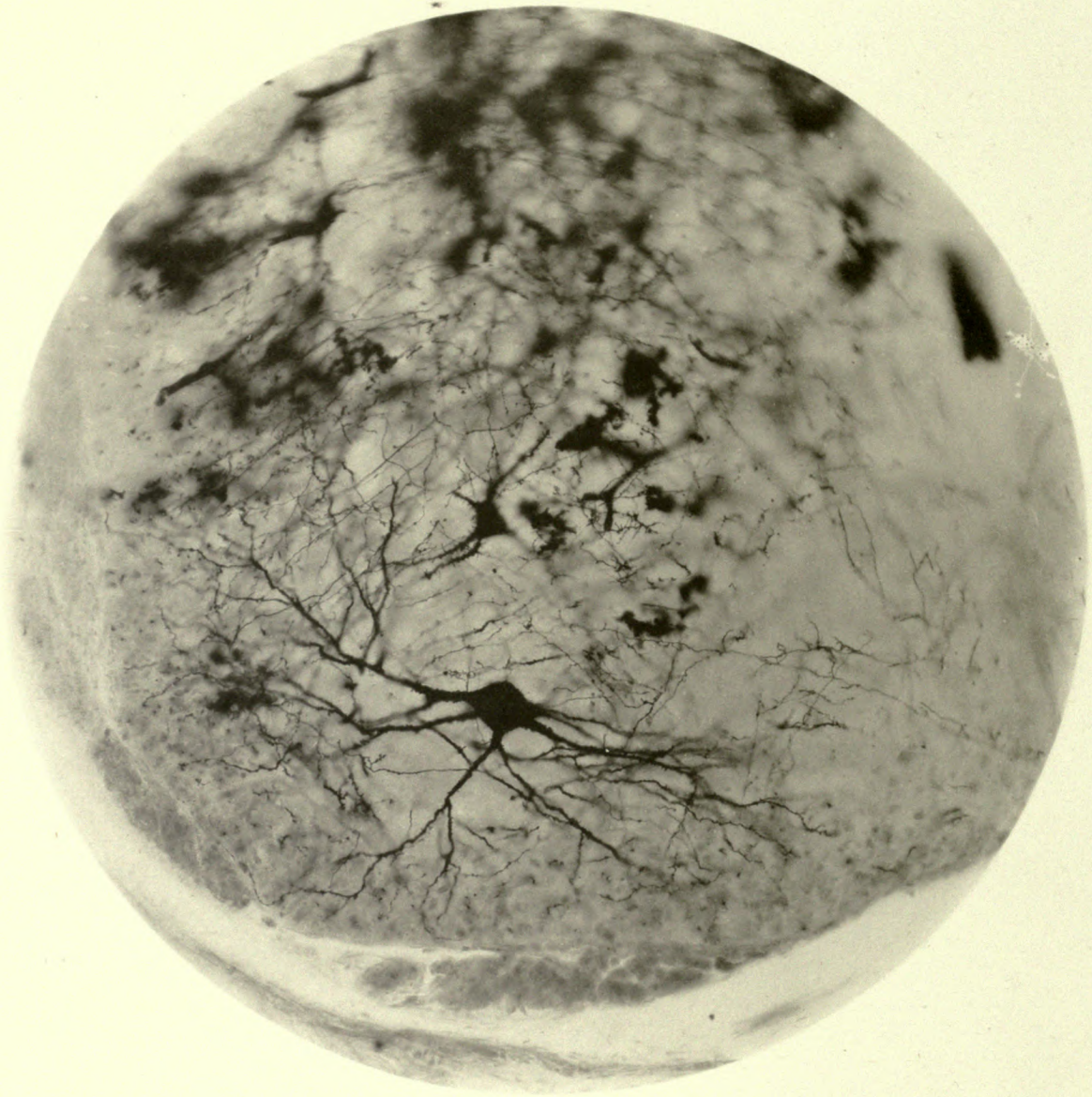CELLS.   X 190 DIAM.

PLATE IV.

LARGE CELL OF THE ANTERIOR HORN OF THE SPINAL CORD OF A CHICK EMBRYO, SHOWING NU-
MEROUS DENDRITES WITH SUB-DIVISIONS. A FINE TERMINAL BRUSH OR ARBORIZATION, THE END OF A
COLLATERAL IS SHOWN JUST BELOW THE LOWER OF THE TWO DENDRITES PASSING TO THE LEFT.
X 190 DIAM.

PLATE V.

There are two varieties of neuraxons which were first distinguished by Golgi. These differ in their course and destination. (1) From some cells the neuraxon proceeds in a long course, giving off collaterals, but preserving its identity till it reaches its destination. It may end in another distant part of the nervous system; or in a muscle, which it reaches by way of the motor nerve trunk; or in the skin which it reaches by way of a sensory nerve; or in some organ of the body. When a cell has such a long neuraxon, it is brought into relation, by means of it, with some distant and different part of the body. It is such a neuraxon which proceeds from the cells of the anterior horns of the cord, enters the nerve root, and goes to the muscles, forming a motor nerve fibre. It is such a neuraxon which proceeds from the Clarke column of cells in the base of the posterior horn, and ascending the cord, in the direct cerebellar column, ends in the cerebellum. Golgi classed all cells with such long neuraxons together as his "*first type*" of cells. He affirms that all such cells are of motor function, but this hypothesis is no longer accepted. This type of cells is easily recognized. It is shown, *e.g.*, in Plates IV. and V. in the spinal cord and in Plates XLII. and XLIII. in the cerebral cortex.

(2) There is a second kind of neuraxon which has a short course and divides and sub-divides soon after leaving the cell, thus forming a plexus of fine fibres in the gray matter, and never proceeding in any particular direction to a great distance. Golgi classes cells pos-sessing this form of neuraxon together as a "*second type*." An example of this type is shown in Plates XLV. and XLVI. He affirms that they are sensory cells; that the neuraxons and their branches from such cells unite with one another, forming a fine network or plexus of fibres, and he states that the sensory nerve fibres arise from or terminate in this network. It has been shown, however, by Cajal that no such true network exists. It is known, further, that cells with such neuraxons are to be found in all parts of the nervous system, not particularly in the posterior horns of the cord; hence the sensory character of this type of cell is now denied. No essential functional distinction between cells of the first and second type can as yet be admitted. Cajal has shown that the sensory fibres do not join any such network as Golgi describes, but end in free extremities, and he considers these cells of Golgi's second type as having a sort of associative function. There is but one neuraxon to each cell throughout the nervous system.

The usual termination of the neuraxon in the nervous system is by breaking up into sev-eral fine filaments, forming a terminal brush, each filament ending freely with or without a little terminal knob. Such a termination has already been shown in Plate V. The col-laterals also have free ends with brush-like expansions. Thus the cell preserves its identity in its neuraxon as in its dendrites. It has a wide possibility of distribution of its impulses through the neuraxon, but it never comes into direct continuity with another cell.

Plate VI. shows a group of neurons in the anterior horn of the spinal cord, the intricate interlacing of both dendrites and neuraxons being clearly seen.

It has already been stated that the function of these neurons is motor, each cell group controlling a single muscle. Muscles act in response to two forms of nervous stimulation, viz., reflex and voluntary, and the mechanism. of these different forms of movement requires separate consideration.
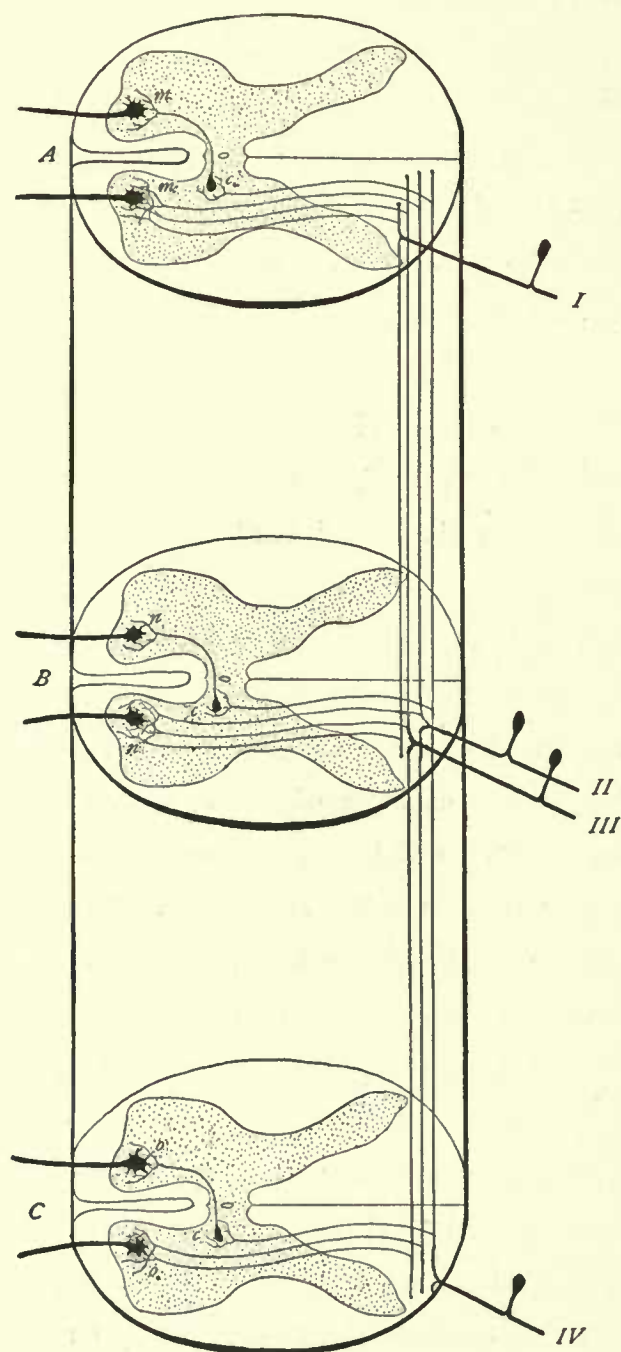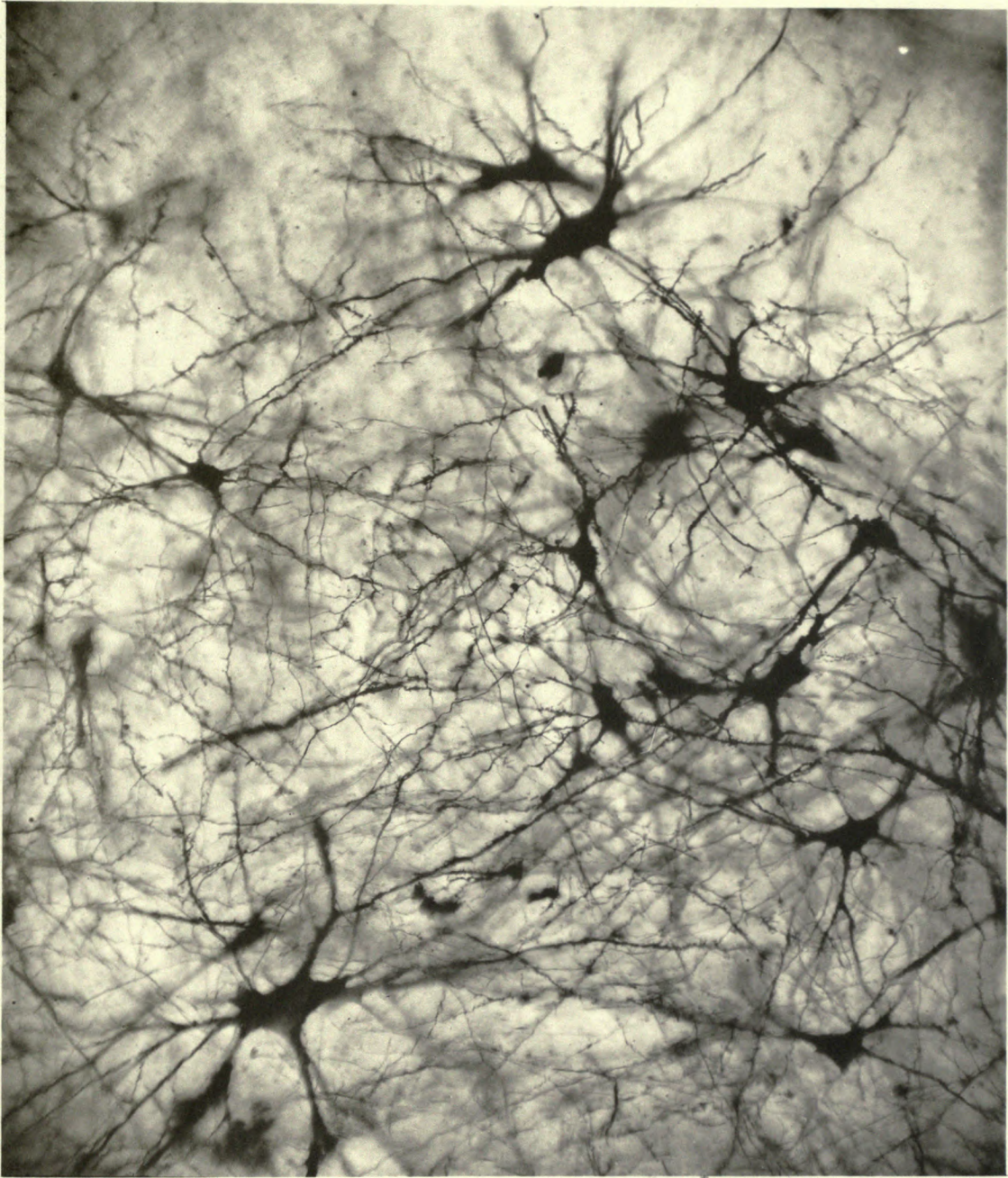
Reflex motion is easily understood by the aid of the diagram, Fig. 3. In this figure three levels of the spinal cord are shown, *A*, *B*, *C*, each containing two motor cells *m*, *n*, *o*, in the anterior horns, and from these motor cells the motor nerve roots issue. Sensory nerve roots I., II., III., IV., are seen to enter the posterior columns and to bifurcate, turning both up and down. The downward branch of I. ends in *B*; the downward branches of II. and III. end in *C*. All send their upward branches to higher levels than those shown. All give off collaterals at all levels, which pass into the gray matter. Some of these collaterals pass forward to the cell of the anterior horn of the same side and terminate in brush-like expansions about the motor cell. A few collaterals pass to the median gray matter and terminate in brush-like expansions about the commissural cell (*c*), whose neuraxon passes to and terminates about the motor cell of the opposite side. A sensory impulse entering the cord at the level *B*, through the posterior nerve roots II. or III., is sent (1) to the motor cell, *n*, on the same side, and (2) if sufficiently intense to excite the intermediate cell *c*, to the motor cell of the opposite side also. The sensory impulse also passes down the cord to level *C*, where it may excite (3) motor cells, *o* and *o*, the latter (4) through the medium of commissural cell *c*. It also passes

FIG. 3.

FIG. 3. — Diagram to illustrate the reflex action of the spinal cord.

A, *B*, and *C*, three levels of the cord. *I*, *II*, *III*, and *IV*, posterior nerve roots entering the cord, bifurcating, ascending and descending, and sending their collaterals and terminations into the gray matter. These terminals end in brushes around the motor cells *m*, *n*, *o*. Some terminals end in brushes around the commissural cells, *c*, which in turn communicate impulses to the motor cells of the opposite side, *m*, *n*, *o*.

A GROUP OF MOTOR CELLS IN THE ANTERIOR HORN OF THE SPINAL CORD OF A FOETAL
PIG, SHOWING NUMEROUS COARSE AND FINE DENDRITES INTERLACING WITH ONE ANOTHER, AND
MANY FINE NEURAXONS GIVING OFF COLLATERALS.   X 190 DIAM.

PLATE VI.

LARGE CELLS OF THE MEDIAN PORTION OF THE SPINAL CORD OF AN EIGHT MONTHS HUMAN
EMBRYO IN LONGITUDINAL SECTION.   A PORTION OF A WHITE COLUMN IS SEEN TO THE RIGHT
OF THE CELLS WITH ITS LONGITUDINAL FIBRES AND COLLATERAL BRANCHES FROM THEM PASSING
INTO THE GRAY MATTER.   X 190 DIAM.

PLATE VII.

up the cord to level *A*, where it reaches and excites the (5) motor cells *m* and (6) *m*. It also passes upward to the basal ganglia, giving rise there to automatic acts, like the cry of pain (7); or to the brain cortex (8); producing there a conscious perception of the sensation. The latter are not represented in the diagram.

The greater the intensity of the sensation, the more marked are its effects in motion. A slight sensation may cause a slight movement on the same side limited to the muscles moved by the cells lying at the level of the cord which the sensory impulse reaches. A very severe sensation may throw into activity the motor cells of both sides at all levels of the spinal cord above and below the level at which it enters. The simple knee jerk is an illustration of the former, the intense rigidity of all the muscles caused by the pain of a lumbago is an illustration of the latter. And all degrees of reflex action between these extremes are possible. Any break in the course of these impulses by a defect in the reflex arc will cause a suspension of reflex action. Hence neuritis by destroying the nerve fibres in the nerve trunk; posterior sclerosis by destroying the nerve fibres in the root zone of the column of Burdach; myelitis by destroying the nerve fibres in their passage through the gray matter; and anterior poliomyelitis by destroying the motor cells in the anterior horn, cause a cessation of reflex activity.

Plate VII. shows a longitudinal section through the spinal cord of a human embryo of eight months, and demonstrates not only the appearance of the large cells of the median region with their dendrites, but also the fine plexus of interlacing nerve fibres, dendrites, and neuraxons in the gray matter, seen on the left; and the longitudinal fibres of a white column, seen on the right. From the fibres of this white column, several collaterals can be seen to come off at right angles and to pass into the gray matter. Around the middle cell in the plate, a few fine terminal filaments of such collaterals can be distinguished with free ends.

Plate VIII. shows one of the intrinsic cells lying in the median gray matter near to the white column. The large size of its body, the great number of its dendrites, and their rich branching are very evident. The neuraxon is not visible. To the right of the plate a longitudinal section through the white column is seen. This column is made up of fibres having the characteristic appearance of axis cylinders, as contrasted with dendrites. Fine collaterals are seen to come off from some of these fibres, at right angles, and to enter the gray matter. These form the means of communication between the fibres of the columns and the cells of the gray matter. They terminate in free extremities.

To the left of the plate several cells are to be seen with fine radiating branches entirely different from the nerve cells and branches. These are the neuroglia cells, which form the supporting framework of the spinal cord.

LARGE POLYGONAL CELL OF THE SPINAL CORD OF A HUMAN EMBRYO, EIGHT MONTHS, IN
LONGITUDINAL SECTION, SHOWING NUMEROUS BRANCHES. TO THE RIGHT OF THE PLATE ARE LON-
GITUDINAL FIBRES OF A WHITE COLUMN WITH NUMEROUS COLLATERALS GIVEN OFF AT RIGHT
ANGLES AND PASSING INTO THE GRAY MATTER. TO THE LEFT OF THE PLATE NUMEROUS NEUR-
OGLIA CELLS ARE SHOWN. X 190 DIAM.
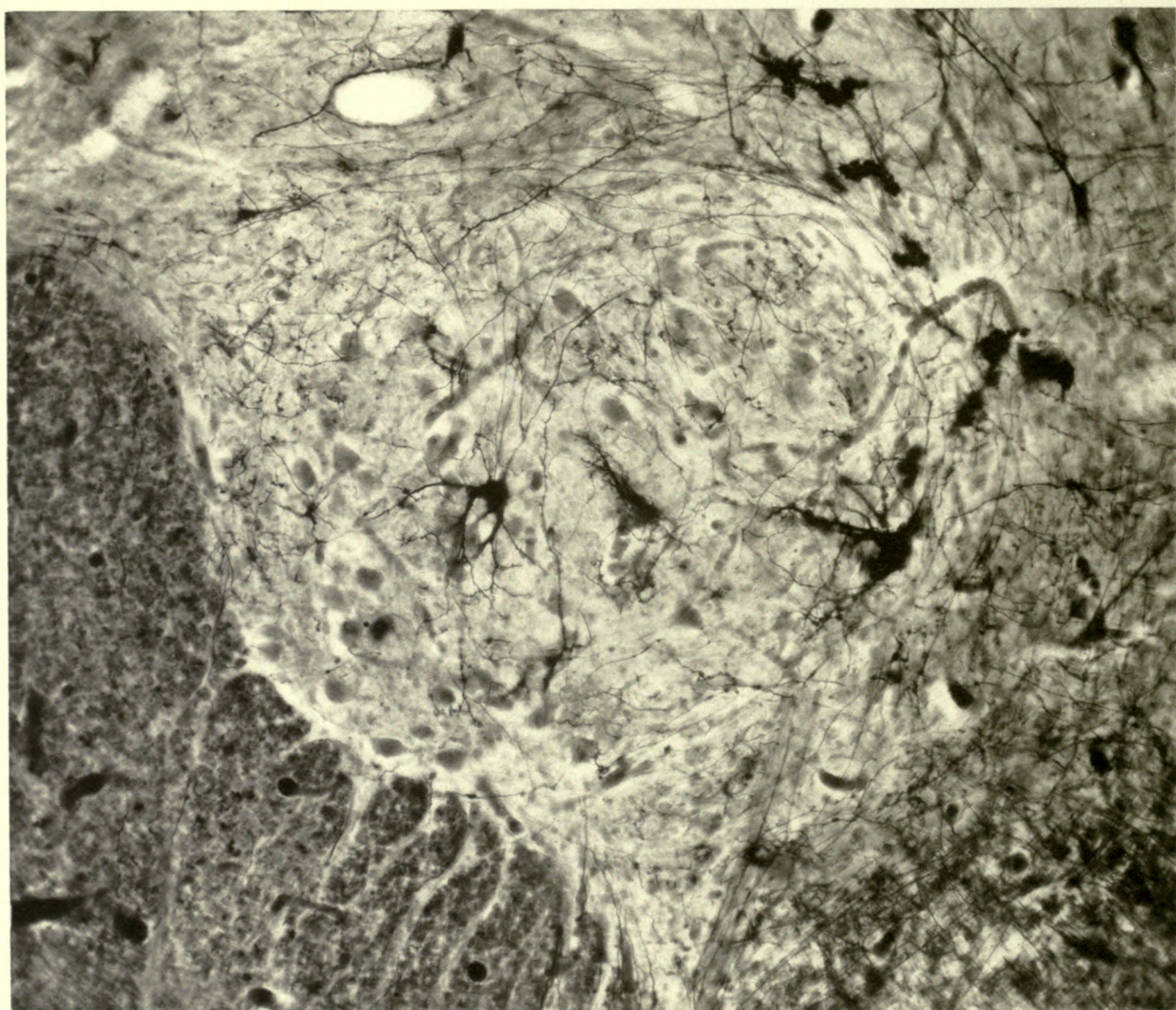
PLATE VIII.

SECTION THROUGH THE POSTERIOR COLUMNS AND BASE OF THE POSTERIOR HORN OF THE
HUMAN SPINAL CORD SHOWING THE CELLS OF THE COLUMN OF CLARKE WITH NUMEROUS DEN-
DRITES AND AXIS CYLINDER PROCESS.   IN THE CELL IN THE CENTRE OF THE PICTURE THE NEU-
RAXON IS SEEN TO PASS FORWARD AND THEN TURN OUTWARD IN ITS COURSE TOWARDS THE DIRECT
CEREBELLUM COLUMN.   X 190 DIAM.

PLATE IX.

While the cells of the anterior horns are collected into distinct groups, those of the posterior horn are usually scattered irregularly through the gray matter. There is, however, one distinct group of cells found at the base of the posterior horn on its median side at certain levels of the cord, viz. the Clarke column of cells. This extends from the mid-lumbar region upward to the lower cervical region. It has also been called the dorsal group of Stilling. A few cells are grouped in the same location in the lower sacral region (Stilling's sacral nucleus), and in the upper cervical region (Stilling's cervical nucleus). The cells of this group are from 45 μ to 90 μ in size. Under some stains they appear to be pear-shaped, with but one projecting process. But the Golgi stain shows them to have both dendrites and a neuraxon.

Plate IX. shows this group of cells, one of which is successfully stained. It is seen to the left of the centre of the plate. It has four dendrites, and a long fine neuraxon which passes forward, and then turns outward through the gray matter. The neuraxons of these cells pass through the median gray matter and through the lateral column to its surface, where they turn upward, and traversing the entire length of the cord, forming the direct cerebellar column, turn outward in the inferior peduncle of the cerebellum, and finally reach that organ (cell d and column V. in Fig. 1, on page 16; also 1 in Fig. 7, page 42). The probable function of these cells is to receive from the posterior root fibres those sensory impulses which are necessary to our appreciation of equilibrium, and without which the nice adjustment of balance is impossible. These impulses are transmitted from these cells to the cerebellum by the direct cerebellar column.

The posterior horn of the spinal cord presents a peculiar structure differing from that of the remainder of the gray matter. This is evident in Plates I. and II. and is more clearly shown in Plate X. It has a peripheral portion and a central portion. The peripheral portion is known as the substance of Rolando, and about its posterior part is a zone of somewhat different appearance known as the spongy layer. The substance of Rolando extends through the entire length of the cord and upward through the medulla and pons, being there in close relation with the termination of the sensory branches of the fifth nerve. It appears, therefore, to have a sensory function. This substance resists many staining materials, and it is only within a short time that its actual structure has been determined by Cajal and Lenhossék. It has a granular homogenous appearance, but they have found that it contains many very small polygonal cells, with dendrites and a neuraxon, the latter coming off from the dorsal side and passing into the lateral column of the cord, where it divides and passes up and down as do the other longitudinal fibres of the cord. About these cells there is a mass of interlacing fibres of most minute calibre, too fine to be stained by ordinary methods.

In the spongy zone, outside the Rolandic substance, lie much larger cells, whose long axis is parallel with the periphery of the cord, and whose dendrites and neuraxons enter the posterior and lateral columns.

The central portion of the posterior horn is made up of a coarser mesh of fibres and of numerous posterior nerve root fibres which traverse it to reach the central gray matter. It contains many of the intrinsic cells already described.

Plate X. shows the entire posterior horn of the cord, including both the substance of Rolando and the spongy zone. The large cell seen near the surface of the cord (at the bottom of the plate), whose long axis is parallel with the surface of the cord, and which has numerous processes passing both into the posterior and lateral columns, and directly into the posterior horn, is the type of cell described by Cajal, and known as the border cell. These cells are supposed to be association cells, and their neuraxon appears to pass uniformly into the posterior columns. The general homogenous structure of the substance of Rolando appears in the plate, but it is seen to be traversed by numerous fibres, which enter the posterior horn from the posterior nerve root. These pass directly to the plexus of nerve fibres which lies deep within the horn near to its base.

THE POSTERIOR HORN OF THE SPINAL CORD OF A HUMAN EMBRYO, EIGHT MONTHS, SHOW-
ING THE SUBSTANCE OF ROLANDO WITH FIBRES PASSING THROUGH IT, THE SPONGY ZONE AND
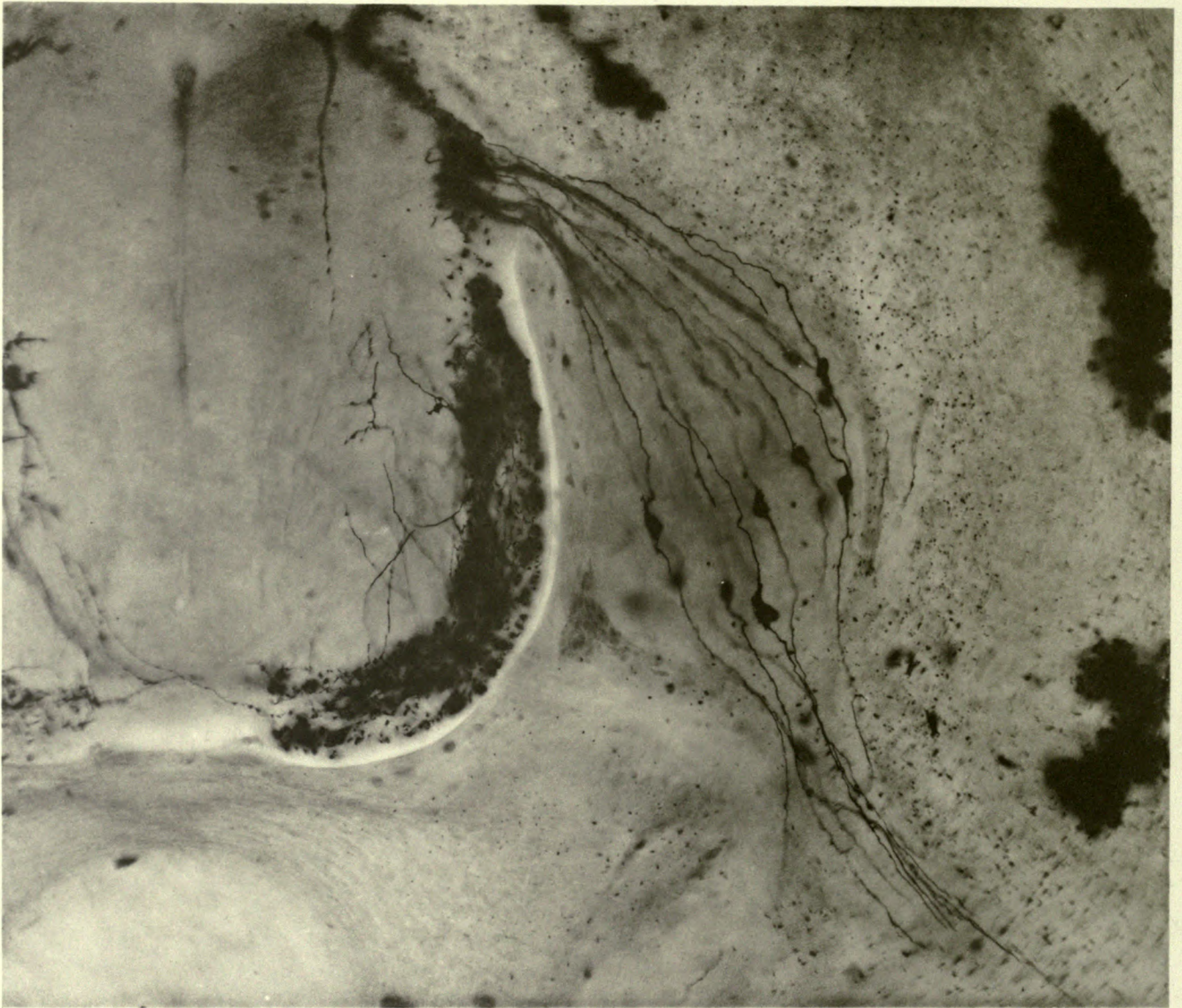A LARGE BORDER CELL ON THE PERIPHERY.   X 190 DIAM.

PLATE X.

SECTION THROUGH A POSTERIOR SPINAL GANGLION AND SPINAL CORD OF A CHICK EMBRYO,
SEVENTH DAY, SHOWING CELLS IN THE POSTERIOR SPINAL GANGLION WITH TWO PROCESSES, ONE
PASSING OUTWARD IN THE SENSORY NERVE, THE OTHER PASSING INWARD AND ENTERING THE SPINAL
CORD.   X 190 DIAM.

PLATE XI.

The spinal cord is made up not only of the neurons thus far described, whose cells lie in it, and of the neuraxons which come down from cells in the brain, but also of a large number of neuraxons which enter it from the posterior spinal ganglia. The researches of His[1] have shown that in these ganglia there develop cells which send out two processes. Plate XI. shows such a ganglion from a chick embryo, containing a number of cells, each with two processes. One process proceeds outward in the posterior spinal nerve, and passes to the skin or to some internal organ. The other process proceeds inward in the posterior spinal nerve root and enters the spinal cord. The latter process is usually smaller in its calibre than the former one, as proven by Retzius.[2] In a later stage of development the body of the cell appears to be pressed to one side, so as to lie not directly in the line of the branches, and then the two branches become fused together, so that in an adult the appearance of the cell is changed, and it looks like a pear with the stem divided and passing in two opposite directions. There has been some discussion as to which of the two branches of these cells is to be called a dendrite and which a neuraxon. As a matter of fact, no distinctive differences are to be seen in the branches, and it is better to regard this type of cell as different from the spinal neurons, and to maintain that these cells have two neuraxons and no dendrites,—especially as both branches receive a medullary sheath on leaving the cell. It is known that sensations are conveyed from the skin to the spinal cord along these branches, and it is evident, therefore, that the distal branch conveys the impulse to the cell, and the proximal branch conveys it from the cell. It is not impossible that the cell has little to do with the function of sensation, and that its only function is to maintain the nutrition of its processes. It is certainly true that if either process is separated from its cell it atrophies in its entire length.

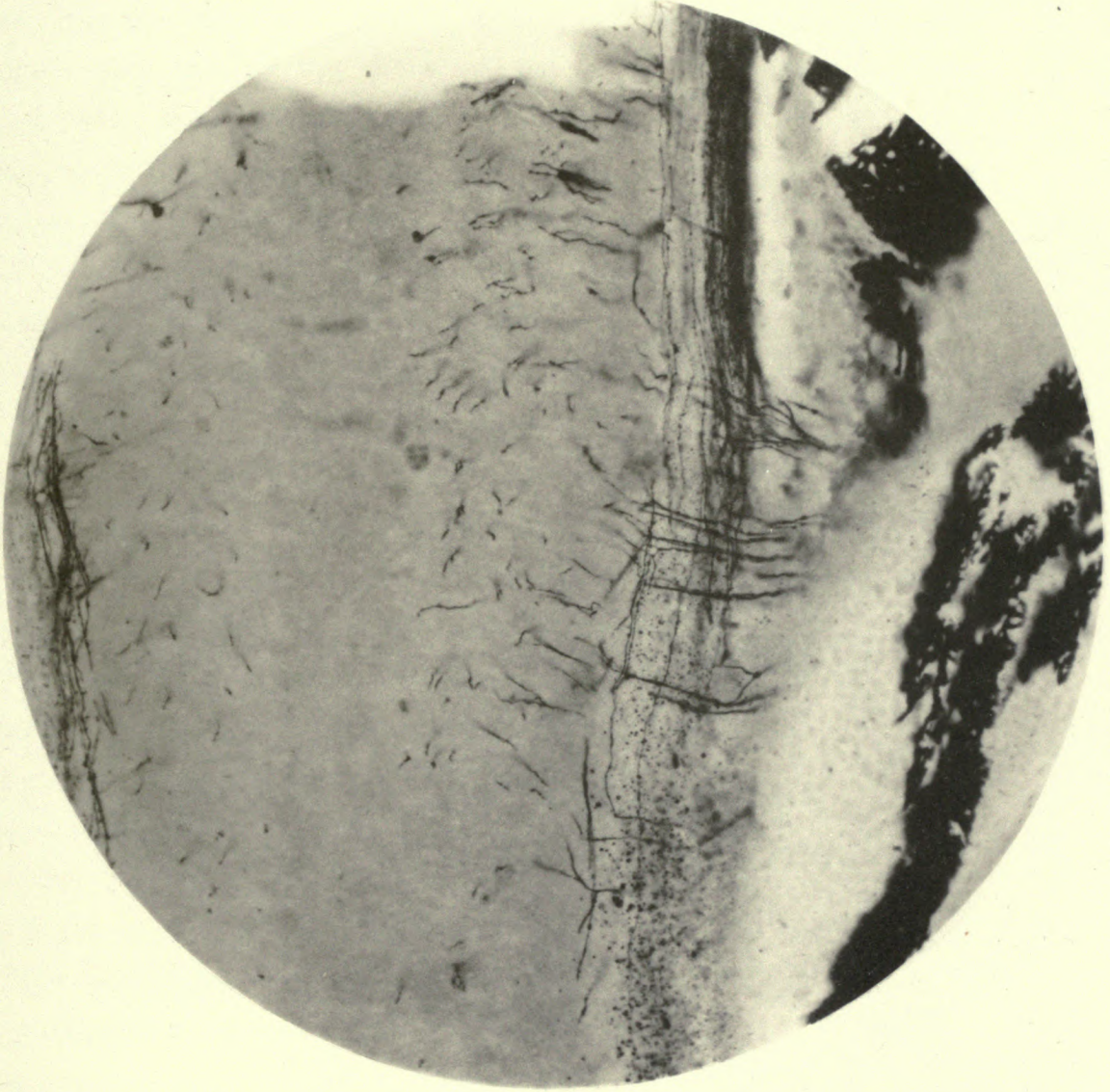[1] W. His, Arch. f. Anat. u. Phys. Anatom. Abtheil., 1887.   [2] Retzius, Biol. Untersuchungen, Stockholm, I. 1890.

The neuraxons which enter the cord from the spinal ganglia pass in partly at the apex of the posterior horn, and partly through the column of Burdach in the portion adjacent to the posterior horn, hence known as the root-zone of the posterior column. On entering the cord each neuraxon divides into two parts, which turn at an angle of 150° to the original direction of the neuraxon, making a Y-shaped division; and these pass up and down the cord. Plate XII. shows this peculiar division of the fibres, as seen in a longitudinal section of the cord through the root-zone. The fibres which pass downward appear to be short, rarely extending downward more than three centimetres. They pass together in a bundle which lies in the antero-lateral part of the column of Burdach, near the posterior horn, and has been termed the comma-shaped bundle, from the shape of its cross-section. Those which pass upward are of indefinite length, many in fact extending all the way to the medulla. Both divisions give off collaterals which enter the gray matter. In a long organ like the cord, which receives 31 pairs of nerves, it is evident that the higher the level, the greater the number of these fibres in a cross-section; for in the cervical region are to be found fibres from every level below it. It has been found that a definite order of arrangement of these long ascending fibres takes place. As each successive nerve root comes into the root-zone, from below upward, it enters near to the posterior horn, and displaces the nerve fibres, already ascending, inward and backward toward the posterior septum. Hence in the cervical cord the fibres from the cervical nerves lie next the posterior horn, those from the dorsal cord are further inward, and those from the lumbar and sacral cord are crowded against the posterior septum.

The arrangement of columns in the cord and their connections with the various cells are shown in the diagram (Fig. 4). *A*, *B*, and *C* are three levels of the spinal cord. I., II., and III. are three sensory nerve roots entering the cord at level *B*. They are seen to bifurcate, to send their branches downwards and upwards to levels *A* and *C*, and to send collaterals into the posterior horns at different levels, some of which terminate about the intrinsic cells of the same side (*h*), and some of which cross in the gray commissure, to terminate about the intrinsic cells of the opposite side (*f*). From these cells a neuraxon proceeds outward to the antero-lateral ascending tract of Gowers (*G*), which passes upward to the brain. Cell *d*, representing the Clarke column of cells, is also shown at the three levels, on the right side only, and its neuraxon ascending the cord in the direct cerebellar column (*D*). Collaterals from the posterior nerve roots terminate around these cells, as has been already shown in Fig. 1, page 16. These collaterals are shown on the left side only in this figure for the sake of clearness. It is thus evident that impulses entering the spinal cord by the posterior nerve roots are not only distributed to the gray matter of the cord itself, as shown

LONGITUDINAL SECTION THROUGH THE SPINAL CORD OF CHICK EMBRYO, SEVENTH DAY, SHOW-
ING THE ENTRANCE OF THE POSTERIOR NERVE ROOTS AND THEIR T SHAPED DIVISION INTO AS-
CENDING AND DESCENDING FIBRES.   X 190 DIAM.

PLATE XII.

in Fig. 3, page 24, representing the reflex action of the cord, but are also sent upward to the brain by three separate tracts; namely, the posterior columns of the side on which they enter, the direct cerebellar column, and the antero-lateral tract of Gowers on the opposite side.

The diagram also exhibits the course of voluntary impulses from the brain downward to the motor neurons of the cord. These impulses, as already described, descend both in the pyramidal tract (P) and in the anterior median column (v). From the descending fibres of these columns fine collaterals come off, which enter the anterior horns of the cord, and terminate in fine terminal brushes about the motor nerve cells. For the sake of clearness, these cells (m, n, o) are shown on one side only. These collaterals are seen to come off at all levels of the cord. The voluntary impulses descending in these columns and thus reaching the anterior motor cells excite them to activity, and the result is a voluntary contraction of the muscle to which their neuraxons pass.

The diagram also shows the existence of intrinsic cells in the cord (i, e), with their neuraxons passing in the antero-lateral column (y, z), and ascending and descending, giving off collaterals which pass into the anterior gray matter of other levels
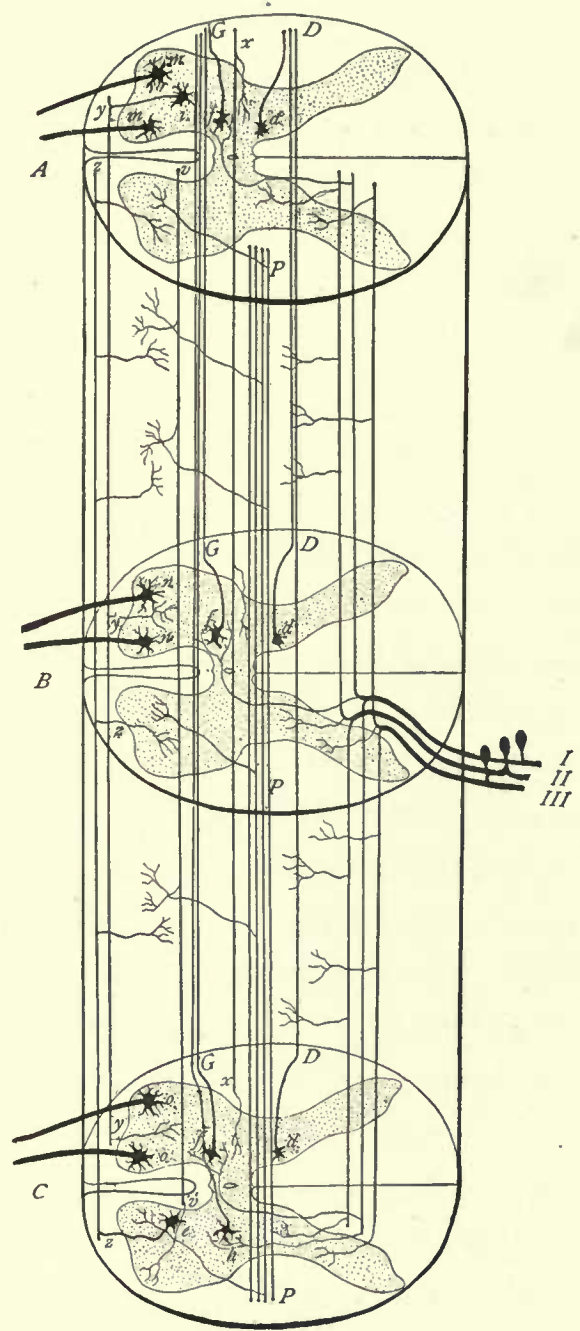

FIG. 4.

FIG. 4. — Diagram to illustrate the transmission of sensory, motor, and association impulses through the spinal cord.

A, B, C, are three levels of the cord. *I, II, III,* are sensory nerve roots entering the posterior root zone at level *B,* bifurcating, ascending and descending, and sending collaterals into the gray matter at many levels. Three such collaterals are shown at *A, B, C,* ending in the posterior horn, and opposite median gray. The collaterals shown in diagrams 1 and 3 are not shown here. The collateral which crosses to the opposite side terminates about the cell *f,* which sends its neuraxon into the column of Gowers, *G,* and thence upward to the medulla. At level *C* a collateral ends about sensory cell *h,* which sends its neuraxon also into *G.* The collateral entering the base of the posterior horn terminates about the column of Clarke on the same side. For the sake of distinctness the cell, *d,* of the column of Clarke is shown on the opposite side with its fibre entering the direct cerebellar column, *D,* and ascending to the cerebellum. *x,* descending cerebellar tract sending its collateral fibres into the median gray. *e,* intrinsic cell of the anterior horn at level *C,* sending its neuraxon into the antero-lateral column, *z,* where it ascends, giving off collaterals, *z,* at levels *B* and *A,* and proceeding upward to the medulla. *i,* intrinsic cell at level *A,* sending its neuraxon into the antero-lateral column, *y,* where it ascends and descends, sending its collaterals, *y, y,* into the anterior horns of levels *B, C.* *P,* pyramidal tract giving off collaterals which pass to the anterior horn of the cord and terminate in brushes about the motor cells. The motor cells, *m, n, o,* are shown for the sake of distinctness on the opposite side. *v,* anterior median column with collateral entering the anterior horn and terminating in brushes around the motor cells.

than the one from which they start. *i* is such a cell, on the right side of the cord at level *A*, with its neuraxon *y* in the right antero-lateral column shown as passing downward; and *e* is such a cell, at level *C* in the left anterior horn, with its neuraxon passing upward. At *x* in the drawing, the descending fibres of the antero-lateral tract, supposed to come from the cerebellum, are seen with collaterals entering and terminating in the median gray portion of the cord.
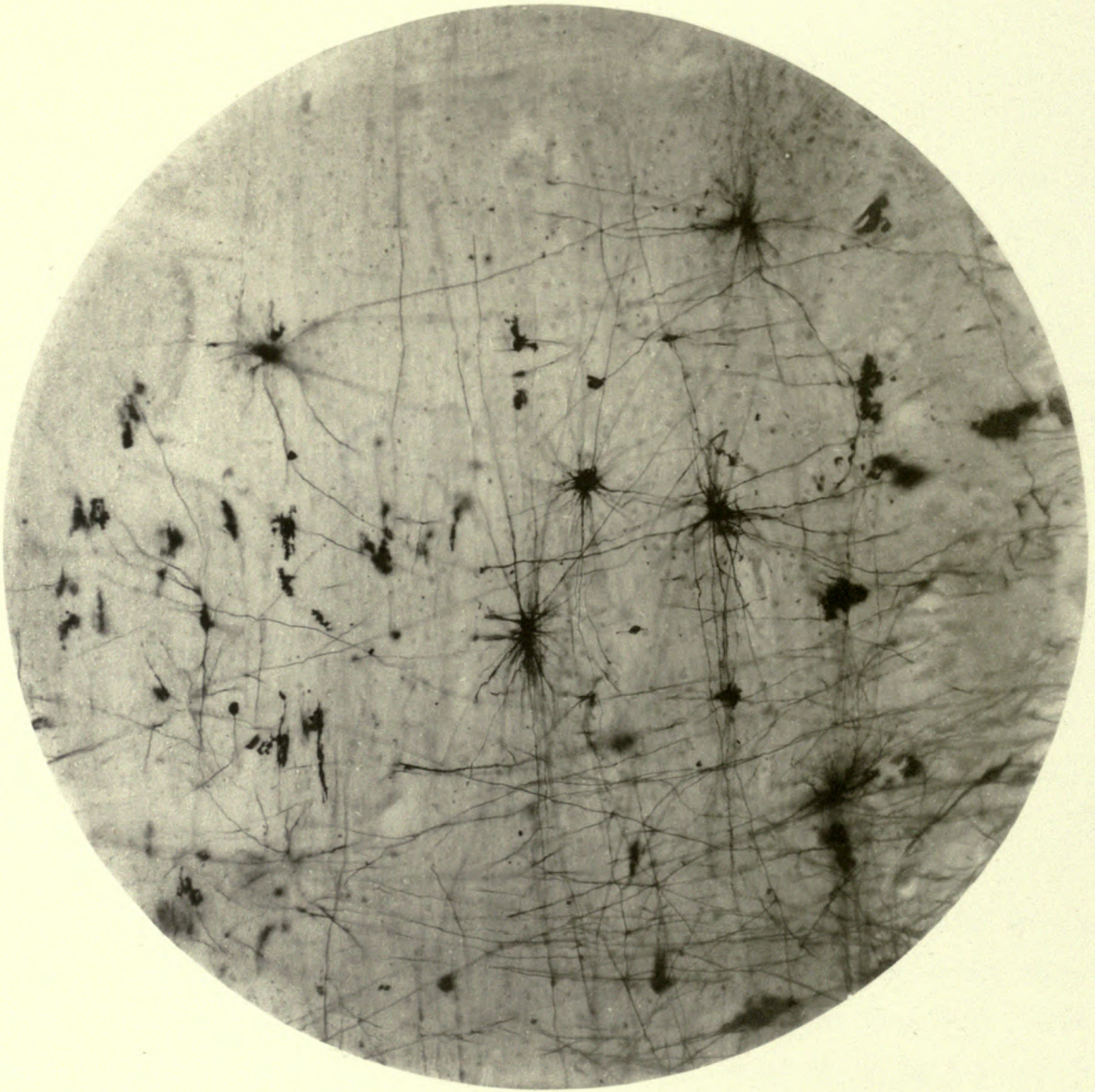
Medulla Oblongata

The cells of the medulla do not differ essentially from those in the spinal cord, excepting in their relative position to the tracts of white matter. The numerous motor cells giving an origin to the motor cranial nerves, are quite similar to the motor cells of the anterior horns of the spinal cord. Throughout the medulla there lie numerous intrinsic cells which are undoubtedly association cells in function, and combine the various complex acts, which are automatically performed by the medulla oblongata. These resemble the intrinsic cells of the cord. Small sensory cells are also found in the substantia gelatinosa of the fifth nerve nucleus of the medulla, similar to those found in the posterior horns of the spinal cord.

All these cells have numerous dendritic branches, and an axis cylinder, which passes upward and downward to the brain or spinal cord, giving off in its course numerous collaterals. The arrangement of these fibres in the medulla is extremely intricate, and does not concern us here. They are clearly traced by Bechterew in his " Leitungsbahnen im Gehirn und Ruckenmark," and by Van Gehuchten in his "Système Nerveux de l'Homme." The histological structure which is especially peculiar to the medulla is the olivary body. This is made up of a thin layer of nerve cells, which layer is highly convoluted, and which is disposed upon the convex surface of the body and around a central mass of fibres, which appear to issue from the olivary body, on one side only. The structure of the olivary body is identical with that of the corpus dentatum of the cerebellum, shown in Plate XX. The olives are connected by means of fibres with the cerebellum, and seem to be in intimate relation with it, as shown in Figure 7, page 42.

NEUROGLIA CELLS IN A LONGITUDINAL SECTION OF THE SPINAL CORD OF A NEW BORN
CHILD.   X 190 DIAM.

PLATE XIII.

Plate XIII. shows a number of cells of the neuroglia in the cord. The neuroglia is admitted by all authorities to be a sort of supporting framework extending through the entire nervous system, giving support to the neurons. It was formerly supposed that the neuroglia was a sort of connective tissue, but the researches of Golgi and His [1] have shown that it originates in the embryo from the ectoderm, — the same layer which develops into the nervous system. The neuroglia develops from the ependymal cells lining the central canal, which send out long fibre-like offshoots extending to the periphery of the cord, and forming a sort of scaffold (Fig. 5). These are shown on the left side of the figure. They do not enter the posterior horns or columns. In addition to this scaffold there develop in the cord spider-like cells with long projections, and these are shown in Plate XIII. The enormous number of these cells, and their grouping in the fœtal cord is shown in Figure 5, taken from Lenhossék. He has shown [2] that these cells develop from the epithelial layer of the embryo, like the nerve cells themselves. A large number of these glia cells cluster about the central canal of the cord, forming a dense interlacing network of glia fibres, known

FIG. 5.

FIG. 5. — (Lenhossék.) Neuroglia cells and fibres of the spinal cord of a human embryo 14 cm. long.

On the left half the long, straight fibres developing from the epithelial cells lining the central canal are shown. On the right half the large number of neuroglia cells developing within the cord and sending their fibres through it are seen.

as the gelatinous substance of Rolando. No special function can be assigned to this region. These glia cells appear to play a considerable part in the pathological processes which go on in the cord. Their abnormal increase gives rise to gliosis in the gray matter, and to sclerosis in the white matter.
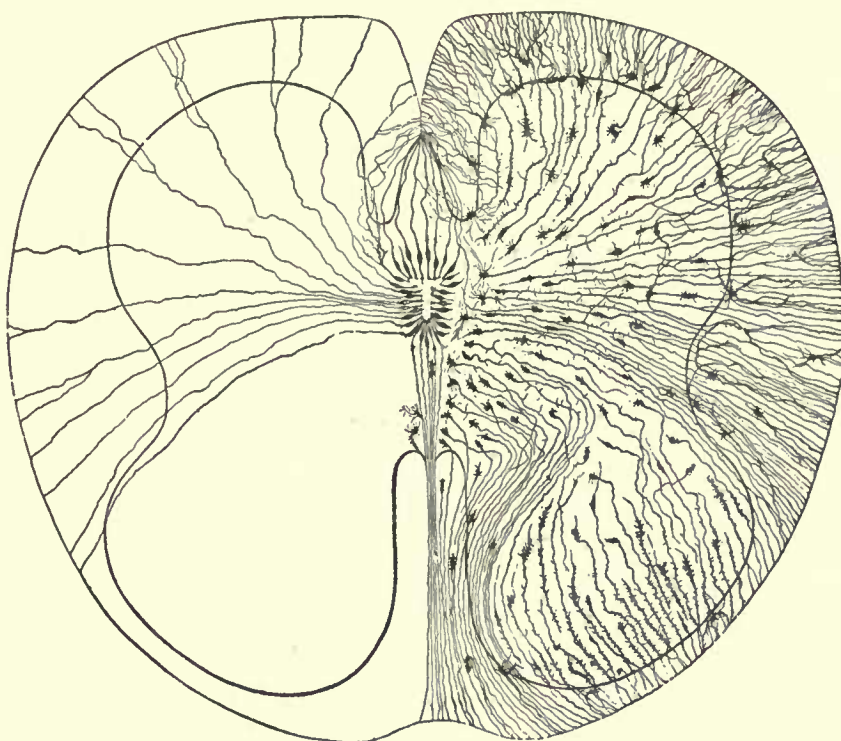
[1] His, Arch. für Anat. u. Phys., Anat. Abth., 1890, s. 103.
[2] M. v. Lenhossék, Verhandl. d. Anat. Gesellsch., 5 Versammlung, 1891, Anat. Anzeiger. 1891, s. 193.

THE CEREBELLAR CORTEX

THE cortex of the cerebellum is, by reason of its numerous fine convolutions, almost as extensive in area as that of the cerebrum. It is made up of two distinct layers of gray matter, between which lie the large Purkinje cells, which form the chief characteristic of this organ. Everywhere beneath these layers of gray matter the nerve fibres collect into white masses, which pass in various directions, bringing the cerebellum into relation with other parts of the nervous system.

Plate XIV. shows the existence of the two cortical layers, and the appearance of the Purkinje cells (*P*)[1] in the adult human brain.

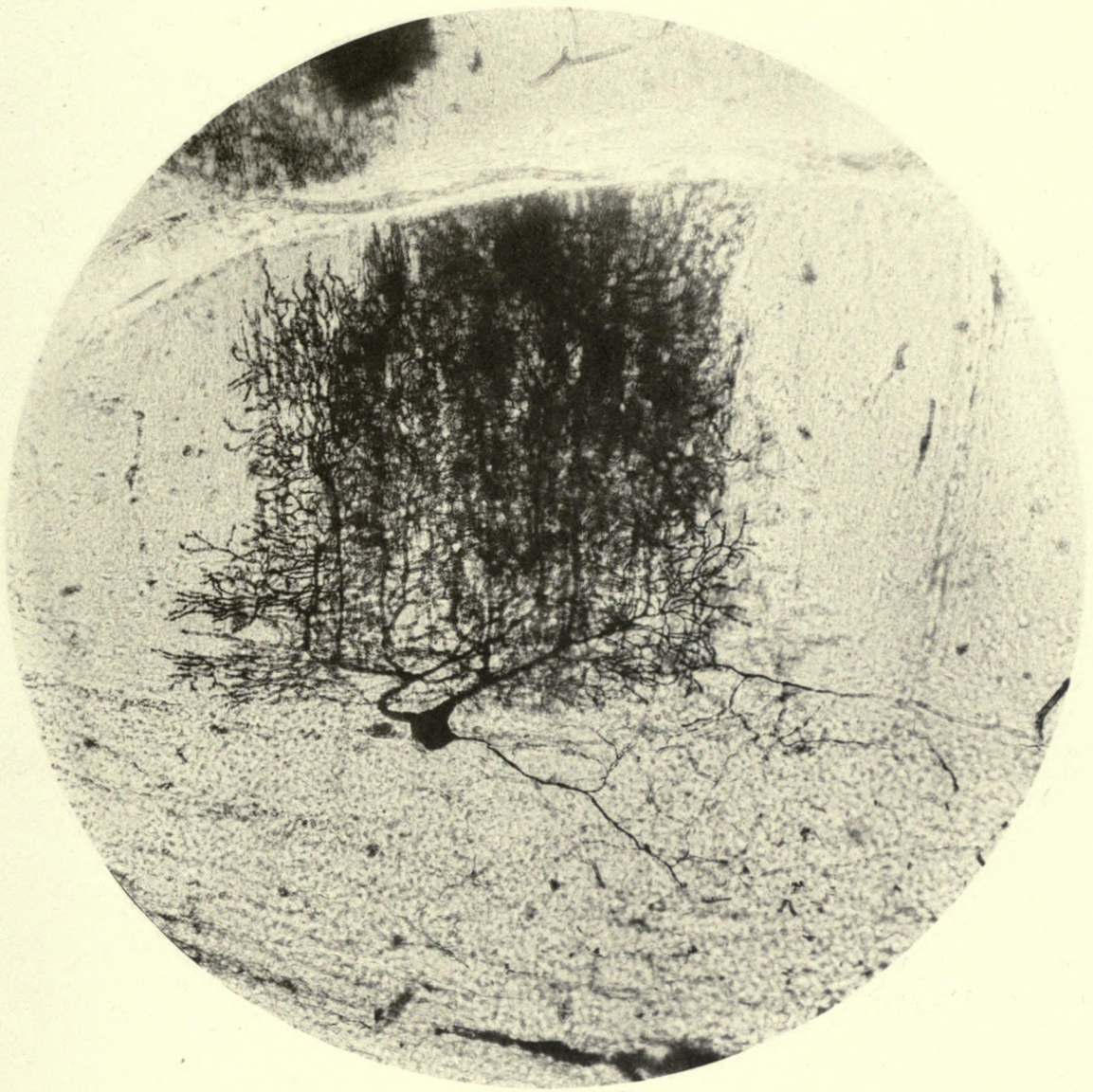The first, or superficial, layer of the cortex has been named the molecular layer.

The second, or deep, layer of the cortex is known as the granular layer.

The Purkinje cell body lies between these layers, and its dendrites pass into the superficial layer, while its neuraxon passes into the deep layer.

The body of the Purkinje cell is round or oval, as shown in Plates XIV. and XV. There are several large protoplasmic extensions of the body which give off numerous branches soon after leaving the body, and these branches present the extraordinarily rich sub-branching which is peculiar to the Purkinje cell. It will be noticed that all these dendritic branches have a rough surface. This is owing to the presence of fine thorn-like excrescences close together on the branch. A high power of magnification shows that these excrescences have clubbed extremities, not being pointed as thorns are. The excrescences have been called gemmules. This extraordinary mass of branches of the Purkinje cell has been termed its arborization. But their arrangement is not exactly like that of a tree, for it is found that these branches all lie in one plane, a plane transverse to the folding of the convolution. Hence if the convolution is cut in a longitudinal plane, the cells and branches are seen only as a thin vertical line. The natural position of the branches may then be compared to the artificial position given to the branches of a plant which has been pressed in a herbarium. As the vast majority of the fine nerve fibres of the molecular layer of the cerebellum have a horizontal and longitudinal direction, it is evident that they can pass through and between

[1] These letters refer to Figure 6, on page 39.

PURKINJE CELL IN ADULT HUMAN CEREBELLUM, SHOWING NUMEROUS BRANCHES IN THE MO-
LECULAR LAYER AND ALSO A LONG AXIS CYLINDER PROCESS WITH TWO COLLATERALS. THIS
PROCESS PASSES THROUGH THE GRANULAR LAYER ON ITS WAY TO THE WHITE MATTER. BASKET
FIBRES ARE SEEN TO THE RIGHT. X 190 DIAM.

PLATE XIV.

PURKINJE CELL IN ADULT HUMAN CEREBELLUM, SHOWING NUMEROUS BRANCHES IN THE MOLEC-
ULAR LAYER AND THE BEGINING OF AN AXIS CYLINDER PROCESS PASSING INWARD INTO THE GRANULAR
LAYER.   X 190 DIAM.

PLATE XV.

the branches of the Purkinje cells, without becoming tortuous. All the dendrites of the Purkinje cells end in free terminations, as is well shown in the plates. The majority of the branches extend quite to the superficial margin of the convolution.

The neuraxon of the Purkinje cell, well shown in the plate, enters the granular layer from the side or base of the cell, and passes through it to enter the white matter. In its passage it gives off several collaterals, which turn backward and ascend into the molecular layer, where they become longitudinal in their direction, branch, and interlace with the dendritic branches of the cell. Cajal supposes that by means of these collaterals the interaction of numerous cells is secured. The neuraxons of the Purkinje cells form the chief constituents of the white tracts of the cerebellum which issue from the cortex. They pass in various directions which will be described later.

To the right of the plate a horizontal fibre is to be seen in the molecular layer, giving off a branch which in turn divides into several branches. This is one of the so-called baskets of the cerebellum — a brush-like or basket-like mass of fibres which surrounds the body of the Purkinje cell. These are also shown in Plate XVIII.

Plate XV. shows another Purkinje cell of the adult human brain with its arborization. The gemmules upon the dendrites are well shown in this plate. The size of the cell is 70 μ. This plate displays the wonderful manner in which the dendrites divide and subdivide until the final terminal filaments are reached. The body of this cell is distinctly pear-shaped, and the neuraxon is clearly seen coming out of the base on one side, but can only be traced a short distance. It has recently been affirmed by Semi Meyer[1] that the gemmules are artifacts of the Golgi method, he having failed to demonstrate their existence by the methylin blue method of staining. This assertion appears to be inconsistent with the uniformity of their appearance in all specimens and with the regularity of their arrangement, both on the dendrites of the Purkinje cells and on the dendrites of the pyramidal cells of the cerebral cortex. They must be considered as actual structures.

[1] Arch. für Micro. Anat., Oct. 1895.

Plate XVI. shows another Purkinje cell with its branches.   The tree-like appearance of the branches is well marked in this plate, and the thorn-like appearance of the gemmules which cover the branches. It will be noticed that the arrangement of the branches conforms to the situation of this cell at the bottom of a sulcus, and that the dendrites are strictly limited to the molecular layer, and do not enter the granular layer at any point. It is only by the Golgi method of staining that the remarkable number and complexity of the divisions of these dendrites has been made known.

The function of the Purkinje cell is undoubtedly to preside over the equilibrium of the body.   When it is considered that the act of balancing requires a nice adjustment of muscles throughout the entire body, that every movement even of eyes and head implies a shifting of the centre of gravity, which must be compensated for when one is standing, by the greater or less contraction on one side or the other of the muscles of the trunk and limbs, and when, moreover, the necessity of constant variations of this adjustment in the motions of the arms, in ordinary gesticulations, in walking, running, dancing, etc., which must be controlled by a competent unconscious mechanism is appreciated, it becomes a matter of less astonishment that the function of these cells is one of the most important in the nervous system, and that their complexity of structure is so great and their connections with other parts are so numerous.

PURKINJE CELL OF ADULT HUMAN CEREBELLUM, SHOWING LARGE NUMBER OF BRANCHES WITH
SUBDIVISIONS WHICH OCCUPY THE MOLECULAR LAYER OF THE CORTEX. THE PECULIAR THORN LIKE
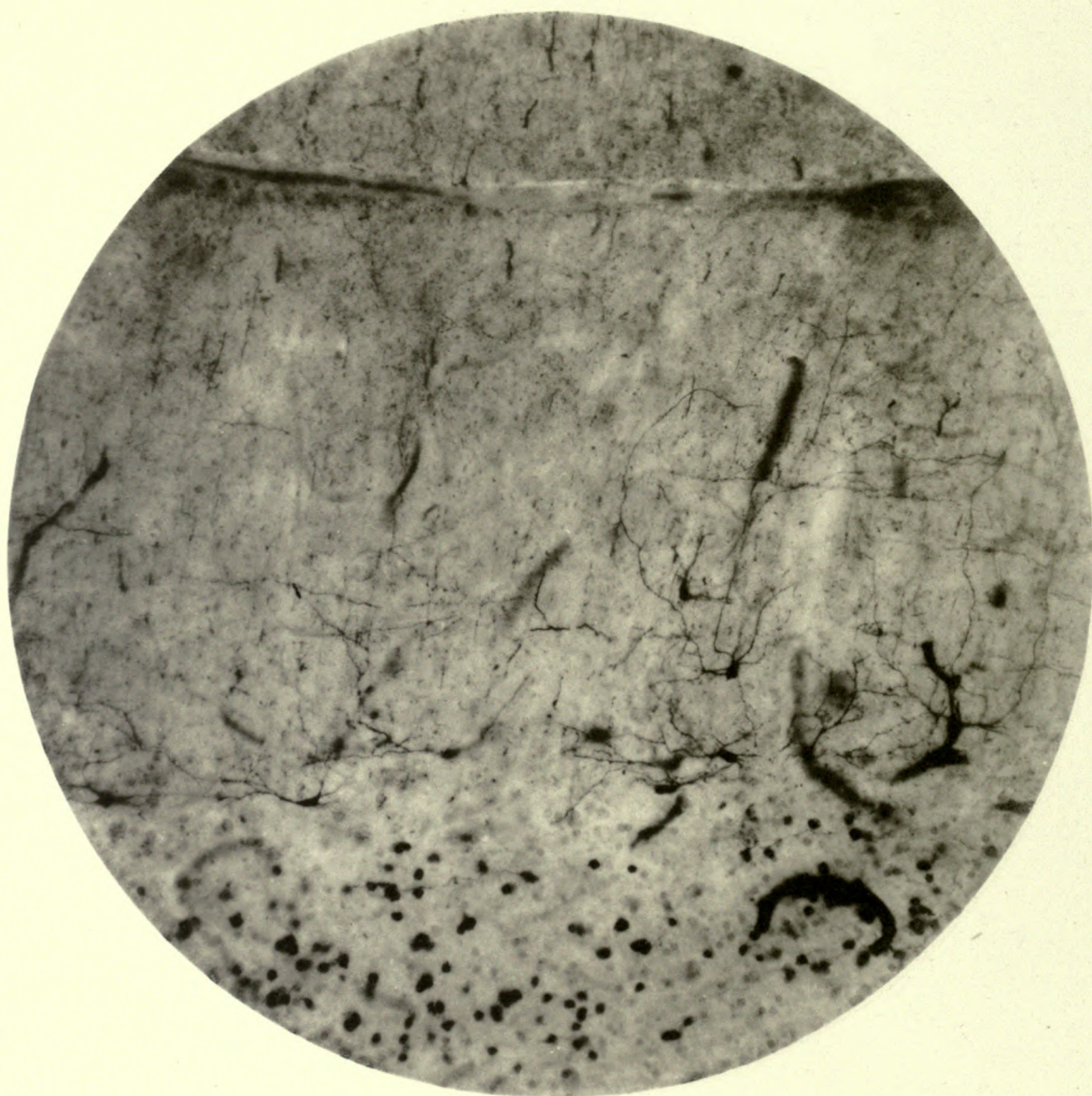EXCRESCENCES ON THESE BRANCHES ARE WELL SHOWN.   X 190 DIAM.

PLATE XVI.

MOLECULAR LAYER OF THE CEREBELLUM SHOWING STELLATE CELLS.   X 190 DIAM.

PLATE XVII.

THE MOLECULAR LAYER OF THE CEREBELLUM

The cells of the molecular layer of the cerebellum are of two varieties. First, the small stellate cells (*S*); secondly, the cells with fibres which enter into the basket-like formation about the Purkinje cell (*B*) (Korbzellen).

Plate XVII. shows the small stellate cells of the molecular layer. They have irregular polygonal bodies with three, four, or more dendrites, and an axis cylinder. The size of these cells is only 10 to 15 μ. The long axis of the body is horizontal in the deeper portion of the molecular layer, but may be directed in any direction in the more superficial part. The dendrites are comparatively short. They divide and subdivide, the majority taking a horizontal direction. The neuraxon is long and gives off numerous collaterals. It appears to pass vertically in the molecular layer only, not entering the granular layer. Its final destination is uncertain. It is impossible to distinguish between the dendrites and the neuraxon in the plate, but a higher magnifying power shows that the longest of the fibres is the neuraxon. Some of the collaterals of the neuraxon can be traced. They usually take a horizontal course after leaving the neuraxon. There are numerous horizontal and vertical fibres shown whose cells are not visible. These together make up a complex interlacing mass of fibres in this molecular layer.
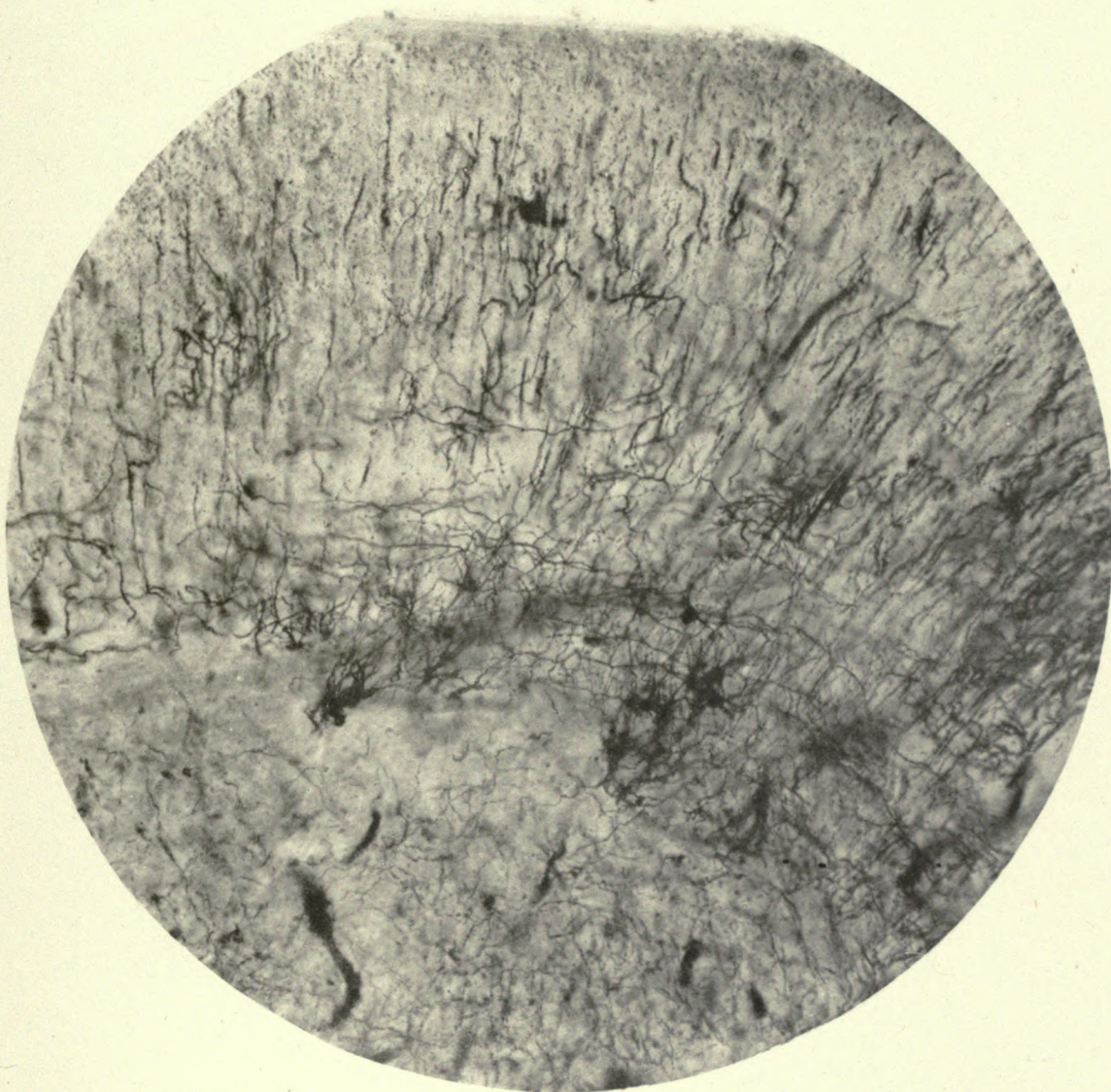
The second variety of cells in the molecular layer is the cell with basket expansion (*B*). These lie chiefly in the deeper part of the layer. They are small cells, polygonal in shape, which give off numerous dendrites and a long neuraxon. This differs from the neuraxon of other cells in being thick and irregular in size. From it there arise numerous collaterals, which take a downward course and end in brush-like expansions, which appear to surround the body of a Purkinje cell. The name "basket cell" is given to these cells because the ends of their collaterals appear to enclose the body of the Purkinje cell as in a basket. It would be erroneous to suppose that the fibres intertwine as do the straws of a basket. The size of these cells is about 20 μ. A doubt has arisen that the basket fibres are true neuraxons; in fact, some authorities have supposed the basket to be a glia structure. Cajal, Golgi, Van Gehuchten, and Kölliker,[1] however, agree with the view that the baskets are made up of fine nerve fibres.

[1] Kölliker, Handbuch d. Gewebelehre des Menschen, 6te Aufl., 1893. II. Bd., 1ste Halfte.

Plate XVIII. shows the molecular layer of the cortex, its intricate plexus of nerve fibres, and a few of the small polygonal cells which give rise to basket fibres. Cajal and Kölliker do not distinguish these cells sharply from the small polygonal cells, previously described as the first variety of cell. Cajal calls them all stellate cells. It is evident, by comparing Plates XVII. and XVIII., that in appearance there is little difference between the first and second variety of cell. The chief difference lies in their size and in the termination of the fibres. It is extremely difficult in any one preparation to show the basket-like expansion (*b*) about the Purkinje cell, especially in the adult human brain. In this plate, however, one such expansion is well shown, and two others are really present, though the undivided fibres are not easily distinguished in this focus. The fibres become enlarged, diverge, and then again converge, forming almost a spherical basket. These baskets lie on the margin between the molecular and granular layers, hence appear to project downward in the plate into the granular layer. It can readily be imagined that these fibres surround the body of the Purkinje cell.

MOLECULAR LAYER OF THE CEREBELLUM SHOWING STELLATE CELLS WITH BASKET FIBRES,
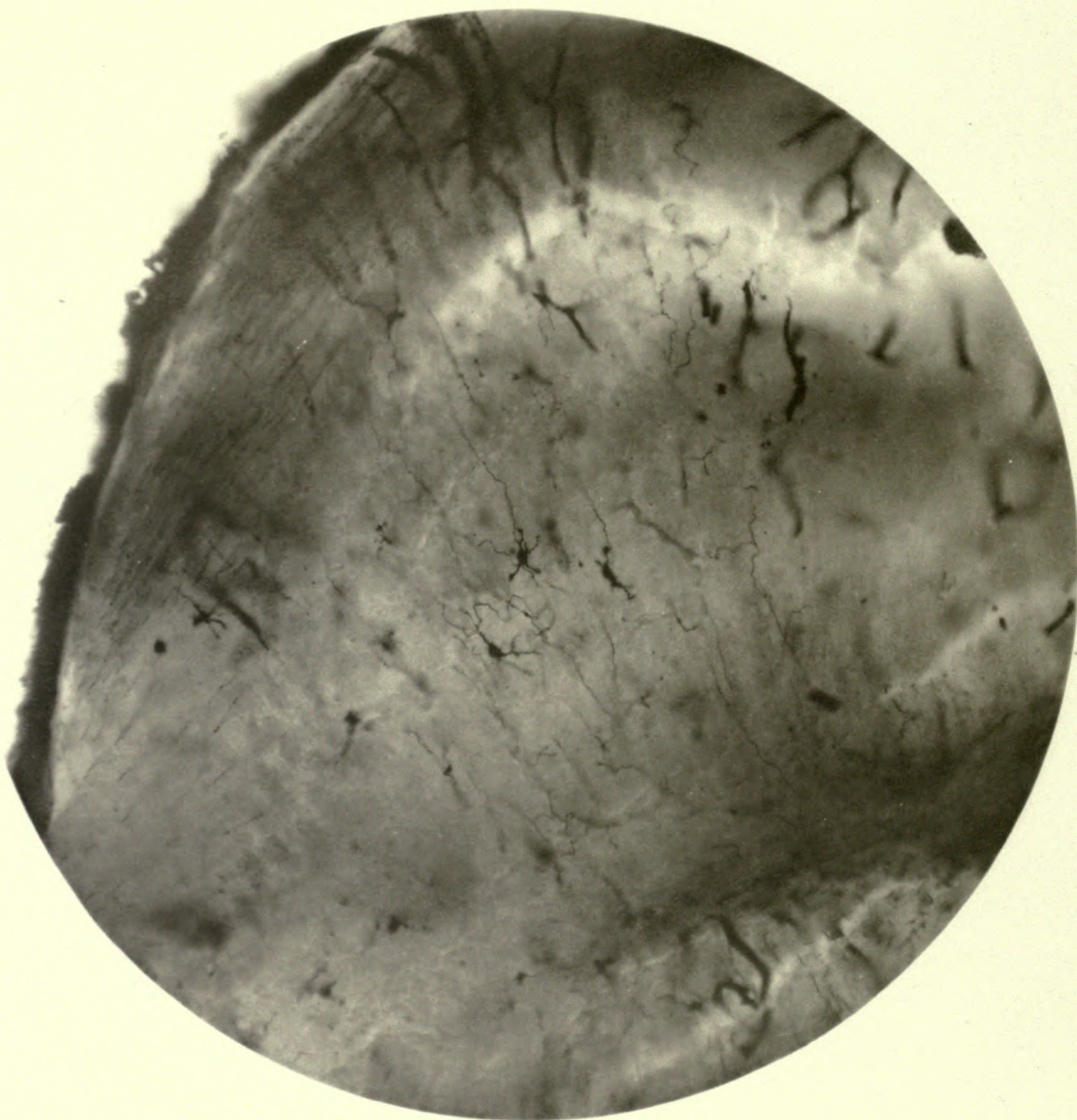AND FINE INTERLACING FIBRES.   X 190 DIAM.

PLATE XVIII.

SMALL GRANULE CELLS IN THE GRANULAR LAYER OF THE CEREBELLUM WITH SHORT DEN-
DRITES AND WITH A FINE AXIS CYLINDER PASSING INTO THE MOLECULAR LAYER. THE LONGITUD-
INAL FIBRES OF THE MOLECULAR LAYER ARE SHOWN IN THE UPPER PORTION OF THE FIGURE.
X 190 DIAM.

PLATE XIX.

The Granular Layer of the Cerebellum

The second, or granular, layer of the cerebellar cortex has about the same thickness as the molecular layer; viz. 1 millimetre. It is made up of very small cells, 5 to 10 μ in diameter (*G*), which are polygonal and have a number of very short dendrites. These cells are very difficult to stain.

Plate XIX. shows three such cells of various shapes and their short, crenated dendrites, which terminate near to the cell in a club-shaped extremity. Kölliker has seen these ends terminating in a fine brush of fibres. Cajal has shown that these cells possess a neuraxon,
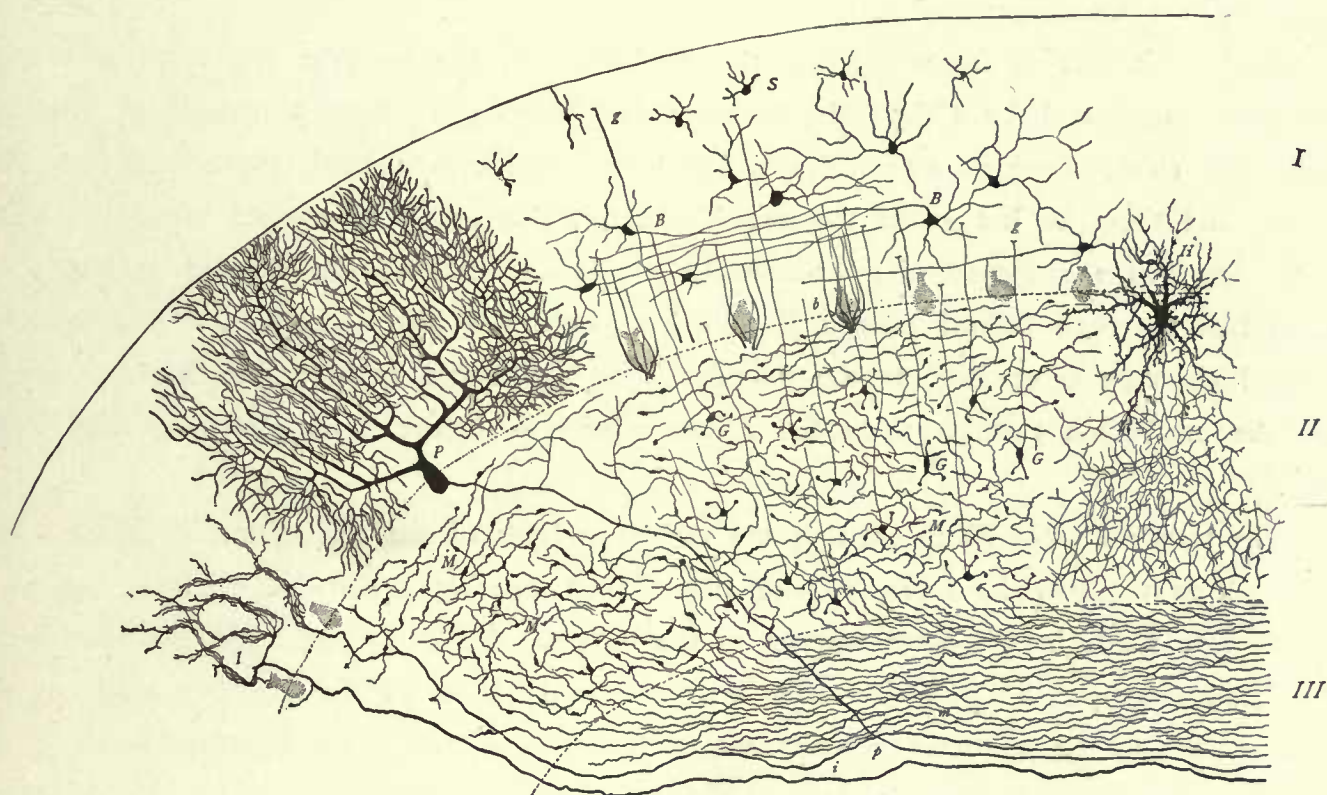

Fig. 6.

Fig. 6. — Diagrammatic representation of a section through the cerebellar cortex. The cells are reproduced from the plates.

I, molecular layer. *II*, granular layer. *III*, white matter. *P*, Purkinje cell with its neuraxon, *p*, entering the white matter. *S*, small stellate cells of molecular layer. *B*, large stellate cells with basket fibres, *b*. These basket fibres surround the body of the Purkinje cell shown in dotted outline. *G*, cells of the granular layer with long, straight neuraxon, *g*, ascending to the molecular layer, and there bifurcating to become tangential fibres. These fibres run at right angles to the plane of section of the plate. *M*, moss-like termination of white fibres, *m*, entering the cerebellum from without. *H*, large Golgi cell of the second type with dendrites in both granular and molecular layers and neuraxon dividing and subdividing within the granular layer. *I*, terminal filaments and fibres, *i*, entering the cerebellum from without and ending around the branches of the Purkinje cells.

which is directed toward the molecular layer (*g*), and after entering it divides in a T-shaped pair of branches, which pass as horizontal and longitudinal fibres in this layer. In the plate one such neuraxon is seen ascending from the middle cell toward the molecular layer. This

plate also shows the large number of horizontal fibres in the molecular layer. The granular layer is made up almost completely of these cells, which are very numerous, lying closely packed together.

Among them are other cells of larger size, first described by Golgi, multipolar, with many dendrites and a neuraxon, which divides and subdivides soon after leaving the cell, forming an extensive plexus through the molecular layer (*H*). These cells belong to Golgi's second type of cell. They are not shown in the plate, but are figured in the diagram (Fig. 6, *H*). The dendrites of these cells enter the molecular layer, but their neuraxon, with its numerous subdivisions, lies in the granular layer.

The mutual arrangement of the various cells of the cerebellum may best be understood by the aid of the diagram (Fig. 6).

The termination of fibres entering the cerebellum in the granular and molecular layers has been investigated by Cajal. He describes in the granular layer a number of branching fibres with short, divergent extremities which have a particularly thick appearance with furry surface, and these he has called the moss-like fibres, since their appearance under the microscope resembles a collection of moss-stems (*M*). This appearance was thought at first to be an artifact, but Van Gehuchten and Retzius have confirmed their existence. This moss-like terminal structure is confined to the granular layer, and seems to bring the impulses coming into the cerebellum through these fibres into relation with the small polygonal cells of this layer.

The termination of fibres entering the molecular layer of the cerebellum is different from that seen in the granular layer. These fibres, after entering the molecular layer, appear to branch very much in the same manner as the cells of Purkinje branch, and the branches of these fibres run parallel with and quite near to the branches of the Purkinje cells, so that there appears to be a second arborization in this layer, enabling the impulses reaching this layer to pass into the Purkinje cell.[1] Cajal has compared this arrangement to that of ivy climbing up a tree, the Purkinje cell being the tree, and these branches the ivy.

[1] Kölliker does not agree with this view, but thinks the branches are less complex than those of the Purkinje cells and that these fibres come rather into contact with the basket cells.

SECTION THROUGH THE CORPUS DENTATUM OF THE CEREBELLUM SHOWING THE CONVOLUTED
APPEARANCE OF THE GRAY MATTER AND THE BUNDLES OF WHITE FIBRES SWEEPING AROUND AND INTO
THE CONVOLUTION. THREE LARGE CELLS OF THE CORPUS DENTATUM WITH NUMEROUS DENDRITES
ARE SHOWN. X 190 DIAM.

PLATE XX.

The Corpus Dentatum of the Cerebellum

Deep within the cerebellum, surrounded on all sides by white fibres, there lies, in each hemisphere, a thin, convoluted mass of gray matter, known as the corpus dentatum. This is made up of nerve cells and of their branches, and appears to be in close connection with the white matter around it. In fact, many fibres in all the peduncles appear to terminate in or to arise from the corpus dentatum, though the chief mass of fibres issuing from it pass into the superior cerebellar peduncle.

Plate XX. shows the appearance of a portion of this body; the convolutions of the gray matter, with the bundles of nerve fibres sweeping around them, or penetrating into them; the large polygonal cells which lie near the surface of one convolution; their dendrites coming off entirely upon the inner side of the cell, *i.e.* upon the side toward the cavity of the convolution and branching in every direction; and the plexus of nerve fibres everywhere present throughout the gray matter. The size of the cells is about 35 μ. They are known to have a neuraxon, but it has not been possible to follow it out or to determine its direction or terminations by the Golgi method. The method of degeneration, however, proves that the chief destination is the red nuclei of the tegmentum, the majority of the fibres decussating with those of the opposite side. It is probable that a part of the fine plexus of nerve fibres in the corpus dentatum consists of terminal filaments of neuraxons coming to this body from a distance, chiefly from the red nuclei of the tegmentum and from the spinal cord.

There are several small groups of cells forming nuclei within the cerebellum, lying in the portion covering the roof of the fourth ventricle, and hence known as the tegmental nuclei, the cells of which resemble those of the corpus dentatum.

It may be added that the olivary bodies and the interolivary nuclei of the medulla are composed of cells of identical appearance and structure with those of the corpus dentatum.

The Connections of the Cerebellum

The origin, course, and termination of the various tracts of fibres which enter and leave the cerebellum and which make up the white matter beneath its cortex may best be understood by the aid of the diagram (Fig. 7).

The cerebellum is connected with the other parts of the nervous system by three peduncles.

I. The inferior peduncle of the cerebellum contains fibres which come from several sources, viz.:

(a) The direct cerebellar column of the spinal cord. The fibres are the neuraxons of the cells of Clarke's column as shown in Fig. 4, page 31. They pass to the cortex of the cerebellum, some of them decussating in the part of the cerebellum which lies above the pons with similar fibres from the other side. No attempt is made in the diagram to show this decussation (1).
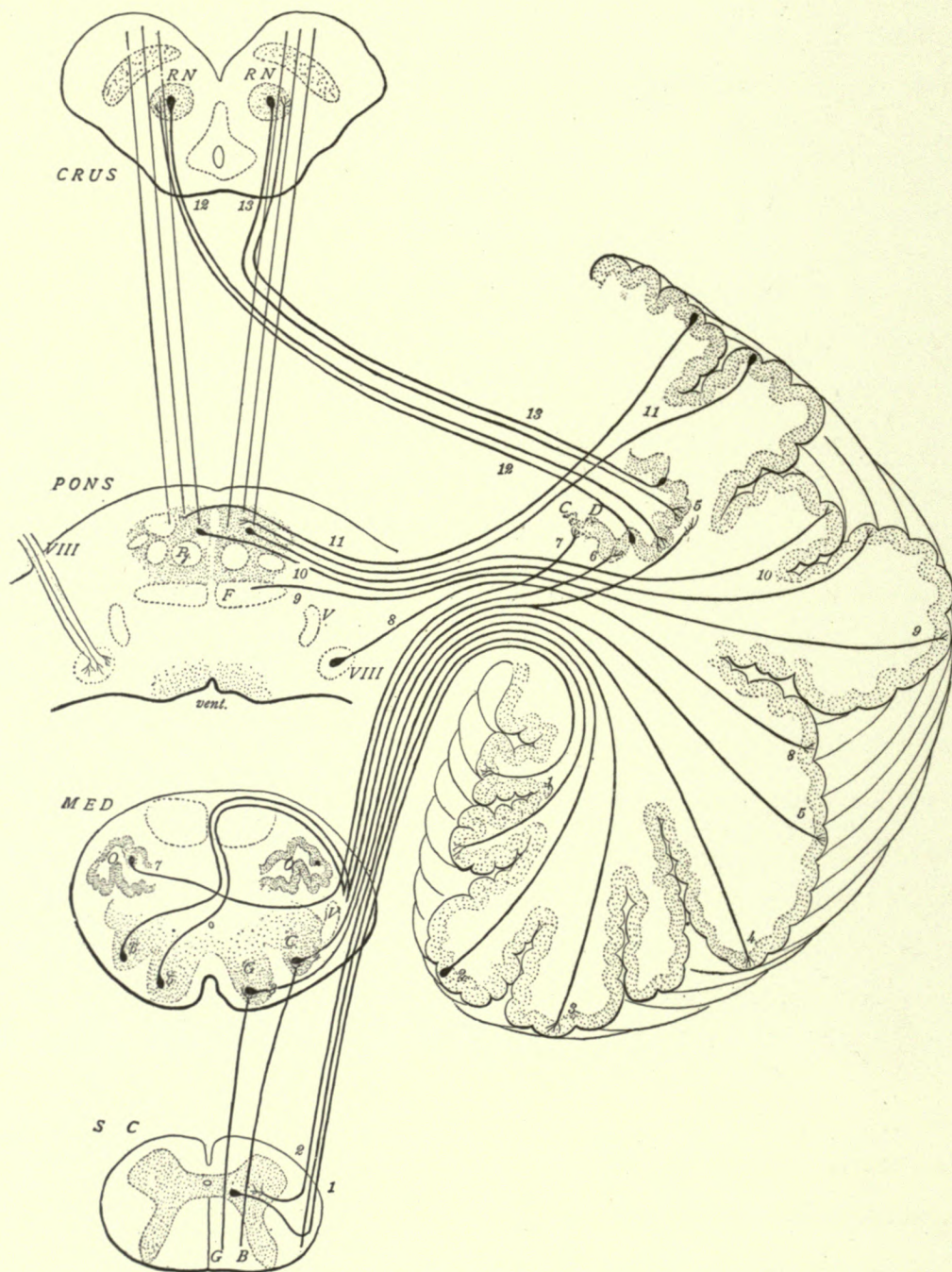

Fig. 7.

Fig. 7. — Diagram to show the connections of the cerebellum.

SC, spinal cord. *G*, column of Goll. *B*, column of Burdach. *MED*, medulla oblongata at sensory decussation. *O*, olive. *G*, nucleus gracilis. *C*, nucleus cuneatus. *V*, fifth nerve. *Pons*, pons Varolii. *VIII*, eighth nerve and its nucleus. *F*, fillet. *Py*, pyramids. *CRUS*, crus cerebri. *RN*, red nucleus of tegmentum. *CD*, corpus dentatum of cerebellum. *1* to *13*, various tracts entering cerebellum from spinal cord, medulla, pons, and crus. For description see text.

(*b*) The descending cerebellar fibres. . These arise from the cortex of the cerebellum and pass down the cord mingled with other fibres in the antero-lateral tract. They end in the median gray matter of the cord. Marchi has shown that these fibres are numerous (2).

(*c*) The nuclei gracilis (*G*) and cuneatus (*C*) of the medulla on both sides, in which the columns of Goll and Burdach end, send a few fibres to the cerebellum. Those on the right side send fibres directly into the right restiform body and thence to the right hemisphere of the cerebellum (3), (4). Those on the left side send fibres across the median line of the medulla in the sensory decussation. These then pass forward in the raphe, pass around the surface of the right pyramid and olivary body (*O*) and join the restiform body, and thus reach the cerebellum (5), (6). These end partly in the corpus dentatum and partly in the cortex.

(*d*) The olivary body (*O*) and interolivary nuclei of each half of the medulla send a large tract across the median line which enters the inferior peduncle and terminates about the corpus dentatum (7).

II. The middle peduncle of the cerebellum contains the fibres which make up the great mass of transverse fibres in the pons Varolii.

(*a*) There is an important bundle of fibres connecting the nucleus vestibuli of the medulla (in which the portion of the acoustic nerve which comes from the semilunar canals ends) with the cerebellum. These lie deep in the mass of fibres of the middle peduncle, and pass to the cortex and nuclei of the vermiform lobe (8).

(*b*) There are some fibres which connect the cerebellar cortex and the fillet as shown by the degenerative method, but in which direction they pass is uncertain, probably upward (9).

(*c*) Those fibres which arise from the gray masses of the pons pass outward to the cerebellar cortex. These have close relation with the fibres which descend to the pons from the frontal lobes of the brain and thus make a continuous functional tract between the frontal lobe of each side and the cerebellar hemisphere of the opposite side, the crossing occurring in the pons (10).

(*d*) Those fibres which arise from the cortex of the cerebellum pass to the gray masses of the ventral part of the pons, from which many new fibres arise which join the pyramids and pass to the medulla or join the descending fibres which pass into the antero-lateral columns of the cord. Some of these fibres decussate in the pons, but the majority end on the side from which they arise (11).

III. The superior cerebellar peduncle contains two sets of fibres passing in opposite directions between the corpus dentatum and the red nuclei of the tegmentum (12), (13). The majority of these decussate under the corpora quadrigemina, but all do not, hence each corpus dentatum is connected with both red nuclei.

In the superior cerebellar peduncle are a number of fibres which go beyond the red nucleus and enter the optic thalamus.

Thus it is evident that the cerebellum has intimate relations with all other parts of the nervous system, — a fact which its principal physiological function, that of adjustment of the equilibrium, would naturally presuppose.
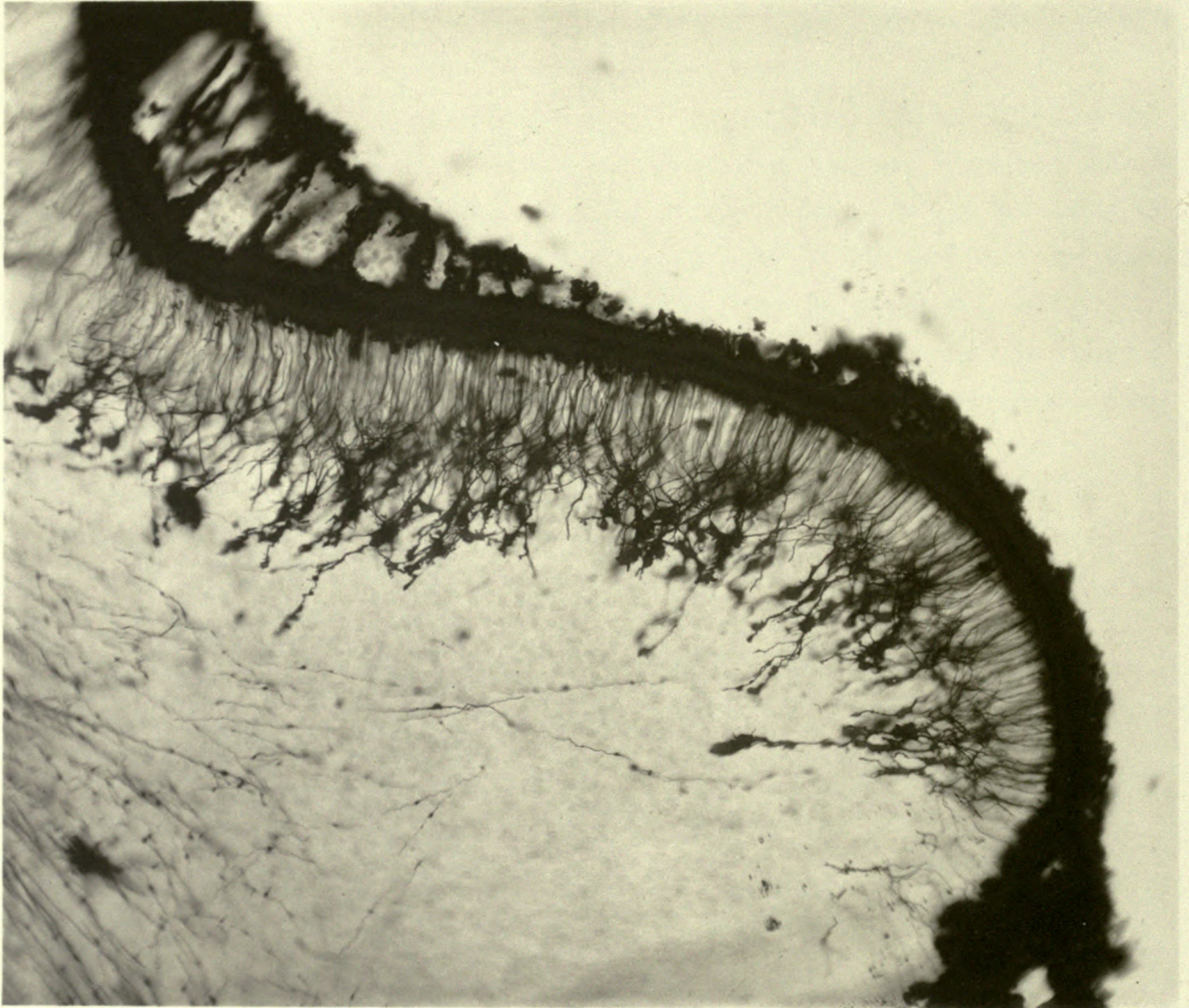
If we review the facts thus far stated, it is evident that there are several ways in which the impulses sent to the cerebellum may awaken a response.

The impulses which reach the moss work of the granular layer set in action the granule cells; these in turn, through their fibres which enter the molecular layer, may set in action either the Purkinje cells through their dendrites or the stellate cells; if the latter are set in action, they may arouse the Purkinje cells by way of the baskets, and then the Purkinje cell may send its impulse outward by its long neuraxon. The impulses which reach the molecular layer by the ivy-like arrangement of fibres come into direct contact with the Purkinje cell, or may act first on the stellate cells and then on the Purkinje cell by the basket fibres.

SECTION THROUGH THE CEREBELLAR CORTEX SHOWING GLIA CELLS AND THEIR VERTICAL
FIBRES FORMING A FRAME WORK.   X 190 DIAM.

PLATE XXI.

Plate XXI. shows the appearance of the framework of neuroglia which gives support to the cerebellar cortex with its cells. The glia cells lie between the two cortical layers, and send outward to the surface numerous fine fibres which form a framework in which the nerve elements lie.
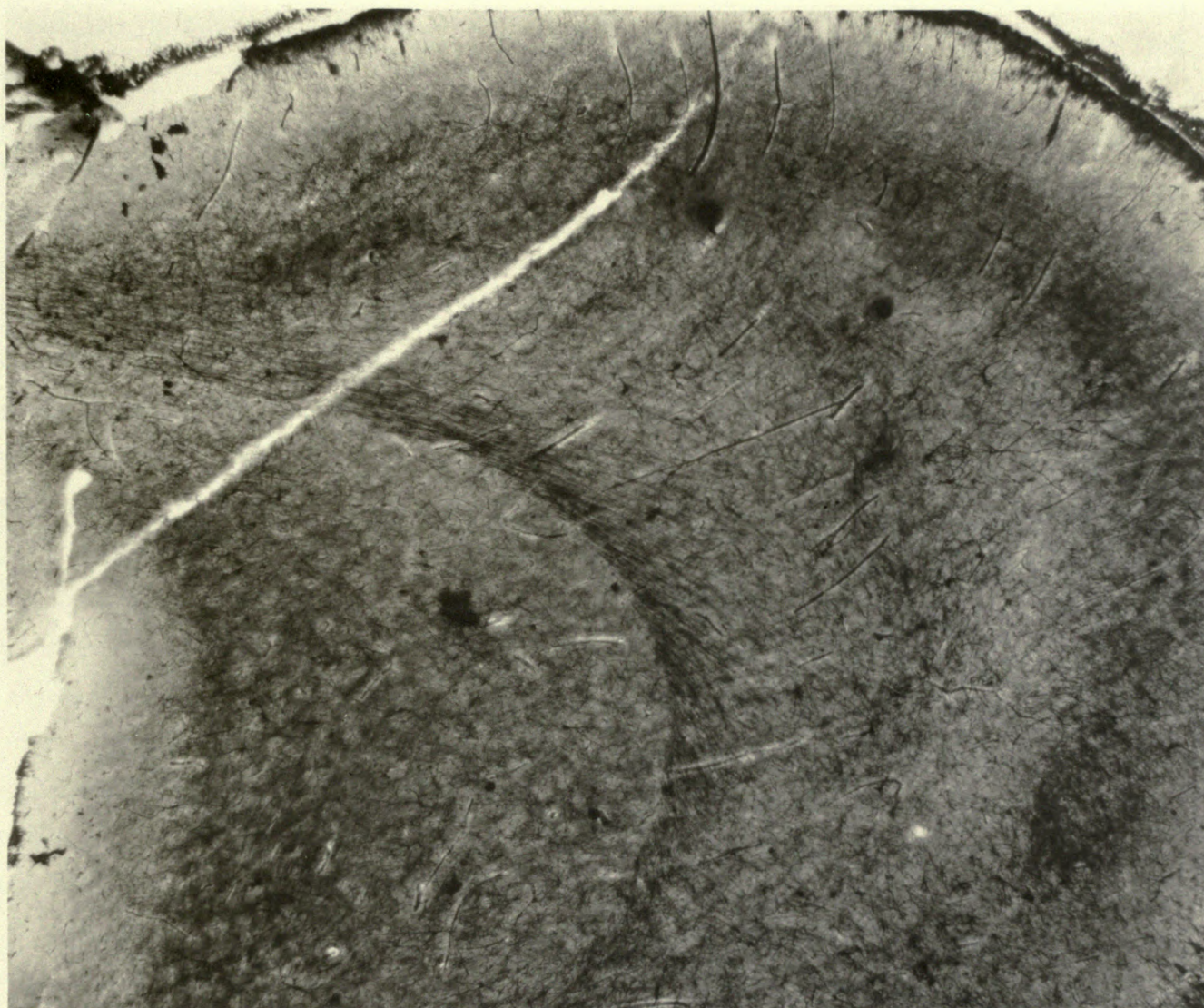
THE CORPUS QUADRIGEMINUM ANTERIOR

THE corpora quadrigemina are four small masses of gray matter lying above the crura cerebri and behind the optic thalamus, and are the smallest of the basal ganglia. They are made up of alternate layers of white and gray matter. They receive numerous bundles of nerve fibres from various parts of the nervous system, and they send out numerous bundles of nerve fibres to the cortex. The corpora quadrigemina posterior receive fibres from the acoustic nerve and from the fillet. They send fibres outward to the temporal region of the brain.

The corpora quadrigemina anterior receive fibres from the optic nerve and from the fillet, and send fibres upward to the occipital cortex of the brain. These ganglia, therefore, are to be regarded as junctions in the passage of nervous impulses, where some impulses are switched off to side tracks, while others pursue their course along the main line.

Plate XXII. shows a transverse section through the right corpus quadrigeminum anterior, its free surface being seen above, and the aqueduct of Sylvius being seen below to the left. It will be seen that everywhere through this section there is a fine interlacing plexus of nerve fibres. It is also evident that there are several concentric layers to be seen.

1. There is a layer of glia cells, which are stained deeply in the plate.

2. The layer of superficial white fibres. In the plate the deeper mass of these nerve fibres only is stained, the surface portion not having taken the stain. The fibres making up this layer come from the optic nerve, their cells of origin lying in the retina. They terminate in the corpora quadrigemina anterior in fine brush-like expansions and free endings.

3. The superficial gray matter. This forms the layer beneath the superficial white matter. It is narrow toward the median line, but broader along the middle of the body. It contains numerous cells, large in size, of various shapes, with extensive branches. These cells are better shown in Plate XXIII.

4. The deep layer of white fibres. Some of these are seen in the plate to have a direction from the median line outward. The majority, however, pass in an antero-posterior direction, and are cut across in this section. They radiate widely into the superficial gray matter, and also enter the deeper gray matter. Many of these fibres are supposed to be

SECTION THROUGH THE ANTERIOR CORPUS QUADRIGEMINUM SHOWING THE VARIOUS LAYERS OF
WHITE AND GRAY MATTER. THE AQUEDUCT OF SYLVIUS IS SEEN TO THE LEFT AND BELOW. X 29 DIAM.

PLATE XXII.

derived from the occipital cortex, being the termination of axis cylinders which arise from the cells there. Others come from, or pass to, the optic thalamus, many crossing the median line in the posterior commissure.

5. The deep gray matter forming the innermost layer is made up of numerous nerve cells small in size. These do not appear to have any direct communication with the visual apparatus, but are in connection with the fibres of the lateral fillet and of the red nucleus.

6. The gray matter surrounding the aqueduct of Sylvius has a homogeneous appearance like that surrounding the central canal of the spinal cord, the so-called gelatinous substance of Rolando, and is made up chiefly of neuroglia.

Von Monakow[1] has shown that when the optic nerve is divided, the superficial white layer and the superficial gray layer undergo atrophy. He has also shown that when the occipital cortex is extirpated, the deep white matter undergoes atrophy, and the superficial gray matter is also slightly affected. Hence, he believes that the visual tract consists of two segments, each of which has a double system of fibres. The first segment extends from the retina to the corpus quadrigeminum anterior (also to the corpus geniculatum externum and optic thalamus). Many of the fibres in this segment arise from cells in the retina, and terminate in a fine network in the corpus quadrigeminum. Others, much fewer in number, arise from the cells in the corpus quadrigeminum and terminate in the retina. The second segment extends from the corpus quadrigeminum (corpus geniculatum externum and thalamus) to the occipital cortex. Many of the fibres in this segment arise from the cells of the corpus quadrigeminum and terminate in a brush-like expansion in the occipital cortex. Others arise from the pyramid cells of the cortex, and terminate in free extremities about cells of the corpus quadrigeminum. The facts established by the investigation of degenerations after lesions, either experimentally produced in animals or found in man, support this arrangement of double tracts, not only in the visual apparatus, but also in the auditory apparatus, and in fact in all the sensory tracts. Hence they must be accepted as proven. A similar arrangement is present in all the tracts entering and leaving the optic thalamus, as will be seen when this ganglion is studied. In the diagram (Fig. 8) these double tracts with their respective origins and terminations are shown.

The function of the anterior corpora quadrigemina is to coördinate the visual impulses which result in ocular movements whether automatic or voluntary. When it is remembered that the eyes will follow a light either automatically during unconsciousness, or voluntarily because of an act of attention, it becomes evident that a double tract, one from the retina, the other from the

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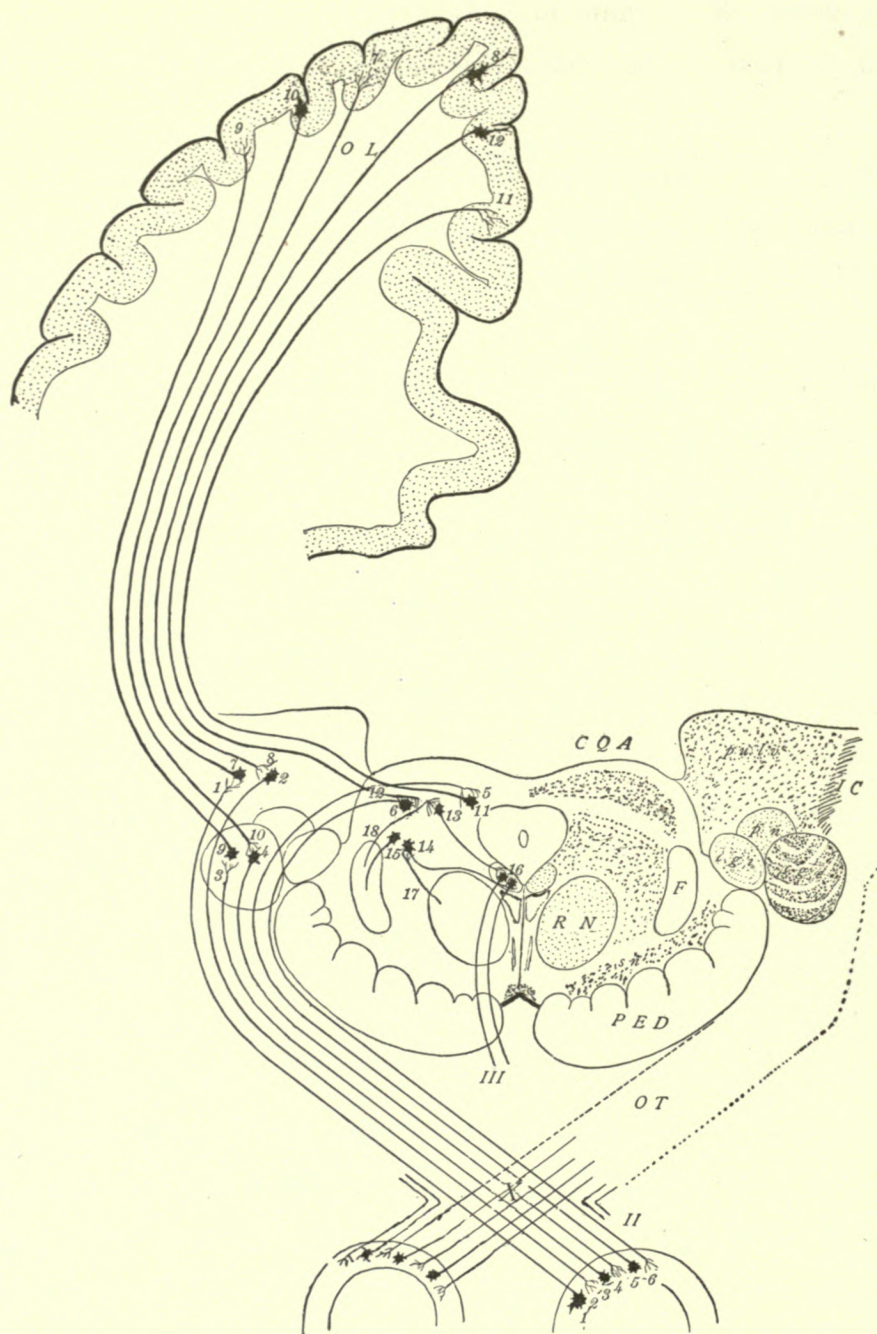[1] C. von Monakow, Archiv f. Psychiatrie, Bd. XX. s. 714.

FIG. 8.

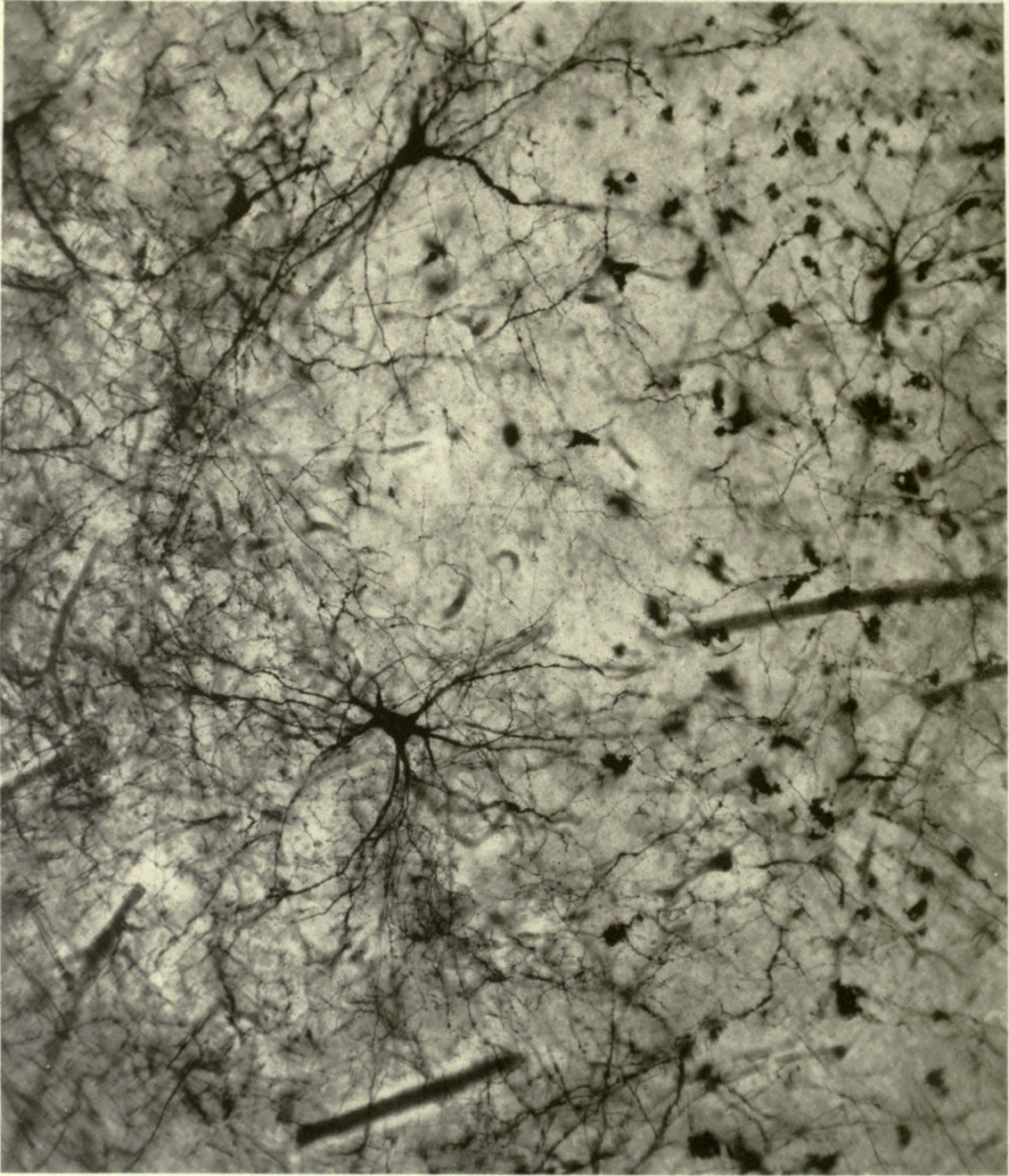FIG. 8. — Diagram of the corpora quadrigemina anterior, *CQA*, showing their connections.

On the right of the figure the superficial and deep masses of gray matter are shown. *pulv,* pulvinar of the optic thalamus. *pn,* posterior nucleus of the optic thalamus lying between the corpus geniculatum externum, *cge,* and the corpus geniculatum internum, *cgi.* *IC,* internal capsule. *F,* fillet. *RN,* red nucleus of the tegmentum. *PED,* peduncle of the cerebrum. *sn,* substantia nigra. *OT,* optic tract. *X,* optic chiasm. *II,* optic nerve. *1, 2,* fibres from the retina to the pulvinar of the optic thalamus. *1,* centripetal. *2,* centrifugal. *7 and 8,* fibres between the optic thalamus and the occipital cortex. *3 and 4,* fibres between the retina and the corpus geniculatum externum. *9 and 10,* corresponding fibres to the occipital cortex. *5 and 6,* fibres between the retina and the corpus quadrigeminum anterior. *11 and 12,* corresponding fibres to the occipital cortex. For the sake of distinctness the decussating optic fibres only are traced. *13,* cell of the superficial gray matter of the *CQA* sending fibre to the nucleus of the third nerve (*16*). *14,* cell of the deep gray of *CQA* sending fibre to third nerve nucleus. *15,* cell of the deep gray of *CQA* sending fibre into the fillet. *17,* fibre from the red nucleus terminating about *14.* *18,* fibre from the fillet terminating about *13.* *OL,* occipital lobe of the brain, with its cortex, containing both cells and terminal brushes of the visual tract.

cortex, is necessary to put in action the coördinating visual apparatus. Hence the double tract established anatomically is a necessity of physiology. But a mechanism is also necessary to correlate the sensory impressions with the motor nuclei of the ocular muscles. This is found in the cells lying in the superficial and deep gray matter of the corpora quadrigemina, among the brushes and cells already described, which send their neuraxons downward to the III., IV., and VI. nerve nuclei, reaching the latter through the posterior longitudinal bundle. These connections are shown in the diagram, Fig. 8.

THE CORPUS QUADRIGEMINUM. LARGE POLYGONAL CELLS OF THE SUPERFICIAL GRAY LAYER.
X 190 DIAM.

PLATE XXIII.

Plate XXIII. shows the large nerve cells of the superficial gray layer of the corpus quadrigeminum anterior. This layer appears to contain the cells which are peculiar to the corpora quadrigemina.

Two cells are shown in the plate quite different from each other. The larger cell is about 60 μ in size. It has six protoplasmic extensions, from each of which several dendrites are given off. These have numerous branches and radiate widely from the cell, evidently passing to a considerable distance from it. There is no neuraxon visible, but other specimens from this region show that these cells possess a long neuraxon which passes out of the body and assumes an antero-posterior direction, entering either the optic tract or the fillet.

The second cell shown is a triangular cell with numerous dendrites which have a very large calibre, a long course in various directions, and give off a few branches in their course. The neuraxon of these cells enters the visual tract and passes to the occipital cortex.

Through the plate the enormous plexus of nerve fibres is evident, and many axis cylinders can be seen easily separable from the dendrites by their finer calibre and straighter course. Many have varicosities, but very few give off collaterals. The general direction in which the majority are passing is from without inward. This plexus belongs to the visual apparatus which has been already described.
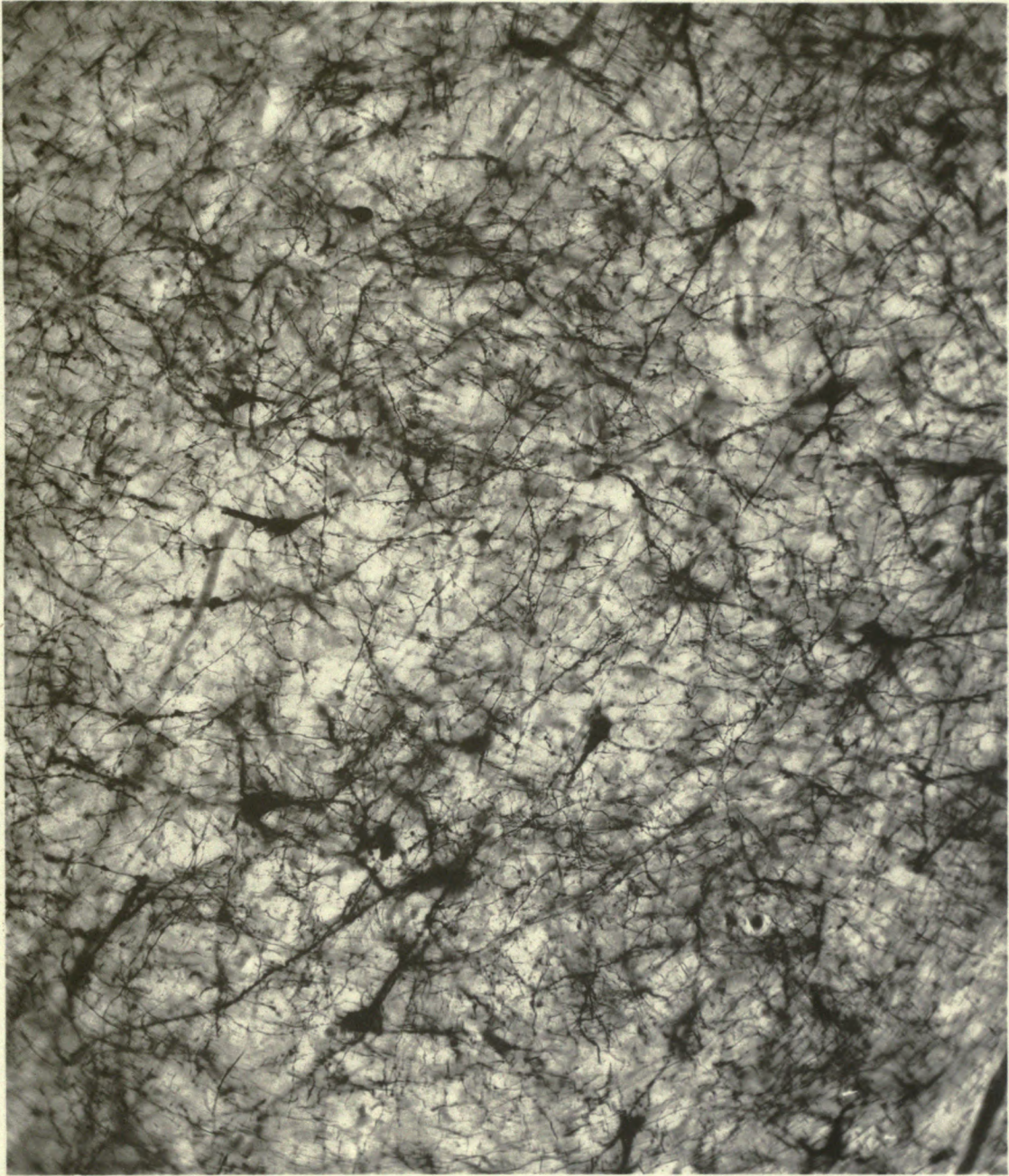
E

Plate XXIV. shows a portion of the deep white layer of the corpus quadrigeminum. It demonstrates the inextricable interlacing mass of nerve fibres which appear to be passing in every direction. Among these fibres, numerous cells are seen of varying size. The majority are triangular with a long apical process pointing outward and downward. These cells have numerous dendrites which give off branches. The direction of their neuraxons is downward and inward to the III. nerve nucleus. They are smaller than those in Plate XXIII., being from 20 to 30 μ in size. Through the mass of fibres there appear to be numberless fine neuraxons with collaterals, and many of them seem to have free ends. Tartuferi[1] and Amaldi[2] have studied the corpora quadrigemina by the Golgi method, but I have not had access to their writings.

The corpus quadrigeminum posterior contains cells and fibres quite similar in appearance to those shown in Plates XXIII. and XXIV. It has a relation to the auditory apparatus quite homologous to that which the anterior body has to the visual apparatus. The fillet conveys the auditory impulses to the corpus quadrigeminum posterior and to the corpus geniculatum internum, and to the posterior nucleus of the thalamus, and from these centres a second tract conveys them outward to the temporal region of the cortex. Von Monakow has shown that in both of these tracts fibres pass in both directions as in the visual tracts.

[1] F. Tartuferi, Sull' anatomia minuta d. eminenze bigemine anteriori dell' uomo, Archivio ital. p. l. malettie nervose; 1885.
[2] P. Amaldi, Rivista sperimentale de Freniatria; 1892.

THE CORPUS QUADRIGEMINUM. SMALL AND TRIANGULAR CELLS AND FINE PLEXUS OF NERVE FIBRES IN THE DEEP LAYER.   X 190 DIAM.

PLATE XXIV.

THE OPTIC THALAMUS

THE optic thalamus consists of a large mass of gray matter, egg-shaped, which lies upon the floor of each lateral ventricle, its upper and inner surfaces being free, its outer surface lying against the internal capsule, and its lower surface being upon the base of the brain and upon the tegmentum of the crus cerebri. Its connections with the other parts of the brain are made partly through its base, and chiefly through the internal capsule. Upon section either horizontally or vertically, it is evident to the naked eye that bundles of white fibres enter it from the capsule, forming apparent divisions between the masses of gray matter. These white bundles have been called the laminæ medullares, and the various divisions of the gray matter formed by the presence of these laminæ have led authors to describe a number of different nuclei in the thalamus. The most recent and most accurate description of these nuclei has been given by von Monakow.[1] He describes the following separate masses of gray matter in the thalamus, but admits that there is no absolute separation between these nuclei at some parts of their circumference. That they are, however, distinct from one another has been established by pathological investigations. Although very little is known with regard to the function of these nuclei at present, von Monakow has shown that each nucleus is in anatomical relation with a definite area of the cortex, and hence the separate function of each nucleus can be in part deduced from the facts known regarding the function of the area of the cortex to which it is joined.

The position of these nuclei in the thalamus is shown in Fig. 9.

The various nuclei are as follows:

1st. The tuberculum anterius (*ta*). This is a distinct hillock of gray matter lying upon the upper free surface of the thalamus far forward and near to the median line. It consists of a number of large nerve cells clustered together. The neuraxons of these cells pass downward to the corpus mammillare at the base of the brain, forming the so-called bundle of Vicz d'Azyr. They there meet the fibres of the fornix, which come from the hippocampus, and thus bring the tuberculum anterius into anatomical relation with the cortex of Ammon's horn.

[1] C. von Monakow, Archiv f. Psychiatrie, Bd. XXVII. s. 640; 1895.

2d. The median nucleus of the thalamus (*med*) lies behind and below the tuberculum anterius, forming a large mass of gray matter which von Monakow divides into two portions, a median (*med, a*) and a lateral (*med, b*) portion. This occupies about one-half of the thalamus in extent, from before backward, being bounded on its lateral surface by the lateral nucleus, and upon its basal surface by the ventral nucleus, and tegmentum of the crura. Von Monakow describes the inner half of this median nucleus as made of larger cells than the outer half, and the two halves are separated from one another by a distinct lamina of white matter. The median nucleus is in anatomical and functional relation with the frontal portion of the Island of Reil and with the second and third frontal convolutions. When

FIG. 9.

FIG. 9. — Frontal sections through basal ganglia to show the nuclei of the optic thalamus. (After von Monakow.)

A, section at junction of posterior and middle thirds of the thalamus. *B,* section at junction of middle and anterior thirds of the thalamus. *OT,* optic thalamus. *lat,* lateral nucleus. *med,* median nucleus. *a,* its median division. *b,* its lateral division. *vent,* ventral nucleus. *h,* ganglion habenulæ. *sn,* substantia nigra. *PED,* cerebral peduncle. *II,* optic nerve. *ta,* anterior tubercle. *Int Cap,* internal capsule. *LN,* lenticular nucleus. *l,* lenticular loop.

these parts of the cortex are extirpated in animals, the nucleus atrophies, and when they are defective in man, this nucleus is defective in development. The cells of the nucleus are shown in Plate XXV.

3d. The lateral nucleus (*lat*). This consists of a large mass of gray matter extending from the anterior extremity of the thalamus backward to the pulvinar and lying against the internal capsule, from which it receives numerous fibres. It is made up of large cells which are shown in Plate XXVI. It is in anatomical relation with the central convolutions.

4th. The ventral nucleus (*vent*). This nucleus lies beneath the median and lateral

nuclei and extends from the anterior backward to the posterior limit of the thalamus, lying very near to the lower portion of the internal capsule. Von Monakow divides this into four sub-nuclei, whose boundaries from one another are very indistinct, but whose independence is assured by the results of degeneration. The anterior part of the ventral nucleus is in anatomical relation with the frontal lobe of the brain in part. The remaining three parts of the ventral nucleus are in relation with the portion of the cortex which lies near the fissure of Sylvius, namely, the operculum, both central convolutions, and the gyrus supramarginalis. The cells of this nucleus are shown in Plates XXVII. and XXVIII.

5th. The pulvinar of the thalamus is the large collection of gray matter lying free upon its posterior and superior surface, and manifestly connected with the optic tract (*pulv* in Fig. 8). This lies behind the lateral nucleus and above the posterior part of the ventral nucleus. It is in direct relation with the occipital lobe of the brain. Upon its posterior and under surface two distinct hillocks of gray matter can be made out by the naked eye; namely, the corpus geniculatum externum (*cge*) and internum (*cgi*), Fig. 8. The corpus geniculatum externum is directly related to the occipital cortex, as are the pulvinar and anterior corpus quadrigeminum. The corpus geniculatum internum is in relation with the first and second temporal convolutions, as is also the posterior corpus quadrigeminum.

6th. The posterior nucleus (*pn* in Fig. 8). A small mass of gray matter belonging to the thalamus lies beneath the pulvinar between the two corpora geniculata. This nucleus is connected with the cortex lying between the temporal and occipital areas.

The ganglion habenulæ is a small collection of cells forming a distinct hillock on the median surface of the thalamus and giving origin to the fibres which pass backward to the pineal gland. The cells of this nucleus are shown in Plate XXIX.

Von Monakow affirms that the tracts connecting these various nuclei with their respective portions of the cortex are made up of two sets of fibres. One set has its origin in the cells of the thalamus and its termination in a brush-like expansion about the cells of the cortex. The other set arises from the pyramid cells of the cortex and ends in brushes within the thalamus. Such a double set of fibres has already been shown in Fig. 8, connecting the pulvinar with the occipital cortex. To establish a further relation between the impulses passing over these double tracts, von Monakow believes that in the thalamus there lie many cells of Golgi's second type, an assertion which the investigations of Marchi confirm.

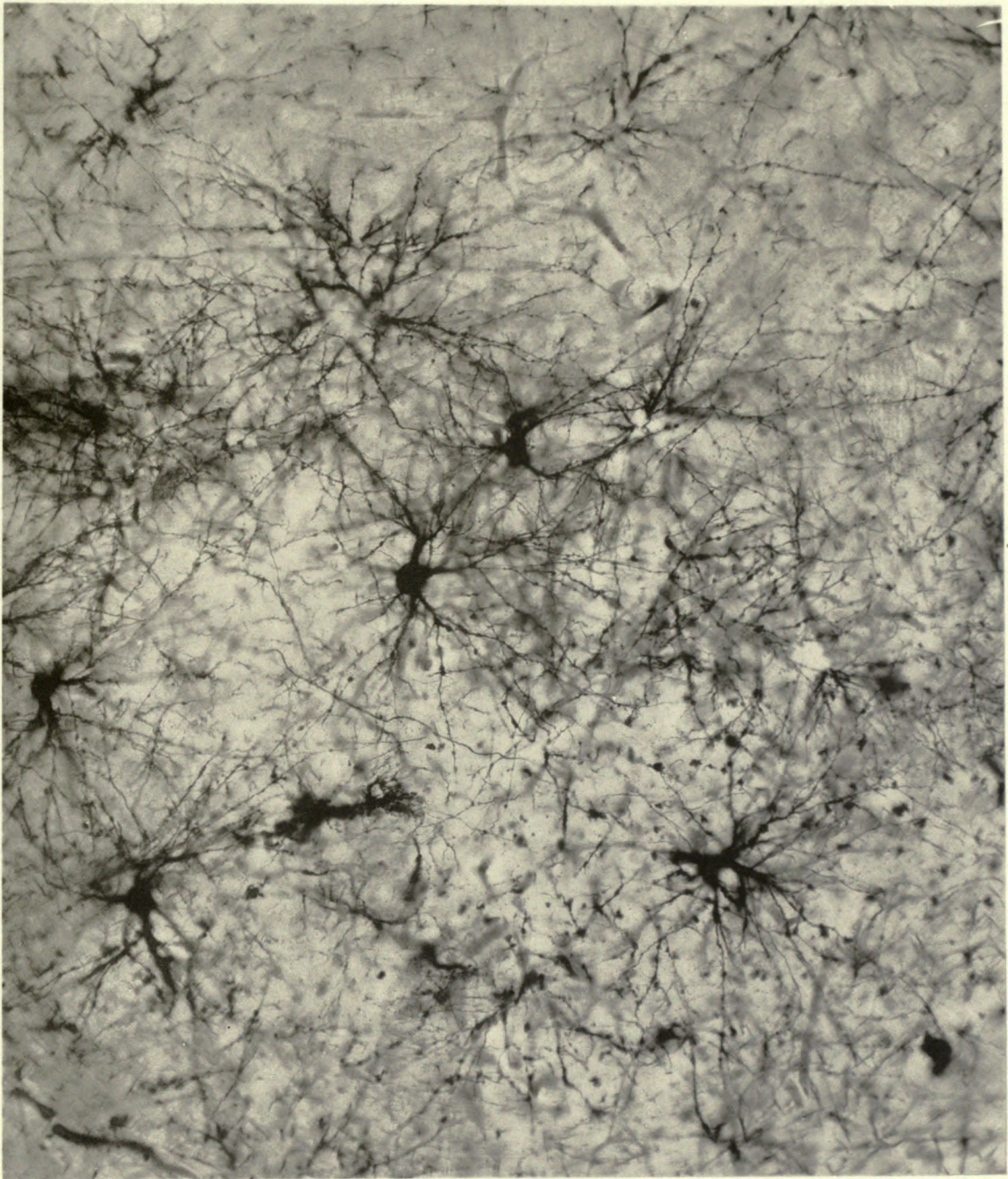There are several varieties of cells in the optic thalamus, and these are shown in Plates XXV. to XXIX.

Plate XXV. shows a form of cell present in many parts of the thalamus, but especially characteristic of the median and lateral nuclei. These cells have a spherical body from which

numerous dendrites come off. The number of dendrites varies from four to ten. No one dendrite is very long, but each gives off very numerous fine branches which radiate in all directions from the cell body, giving an appearance which seems to justify the name, which I propose, of stellate cells. These dendritic branches are short and terminate in free extremities in the thalamus. The interlacing of numerous adjacent dendrites with one another forms a fine plexus of fibres in the gray matter. The neuraxon of the stellate cells arises from the body of the cell and passes off in a straight direction, giving off very few collaterals. The direction of the neuraxon varies in different cells even in the same nucleus. There appears to be no general mass of neuraxons passing together in bundles that can be traced. Yet the existence of the laminæ medullares in the thalamus proves that such bundles do pass through the masses of gray matter, and it is probable that the neuraxons gather into bundles, leaving the thalamus through the internal capsule. Marchi[1] has studied the thalamus by the Golgi method, but his monograph is quite incomplete; he found only two kinds of cells, large and small, and he does not distinguish the nuclei of the thalamus from one another.

[1] V. Marchi, Sulla struttura del thalami optici, Rev. Sper. di Fren.; 1884 and 1887.

MEDIUM SIZED STELLATE CELLS OF THE OPTIC THALAMUS WITH VERY NUMEROUS DEN-
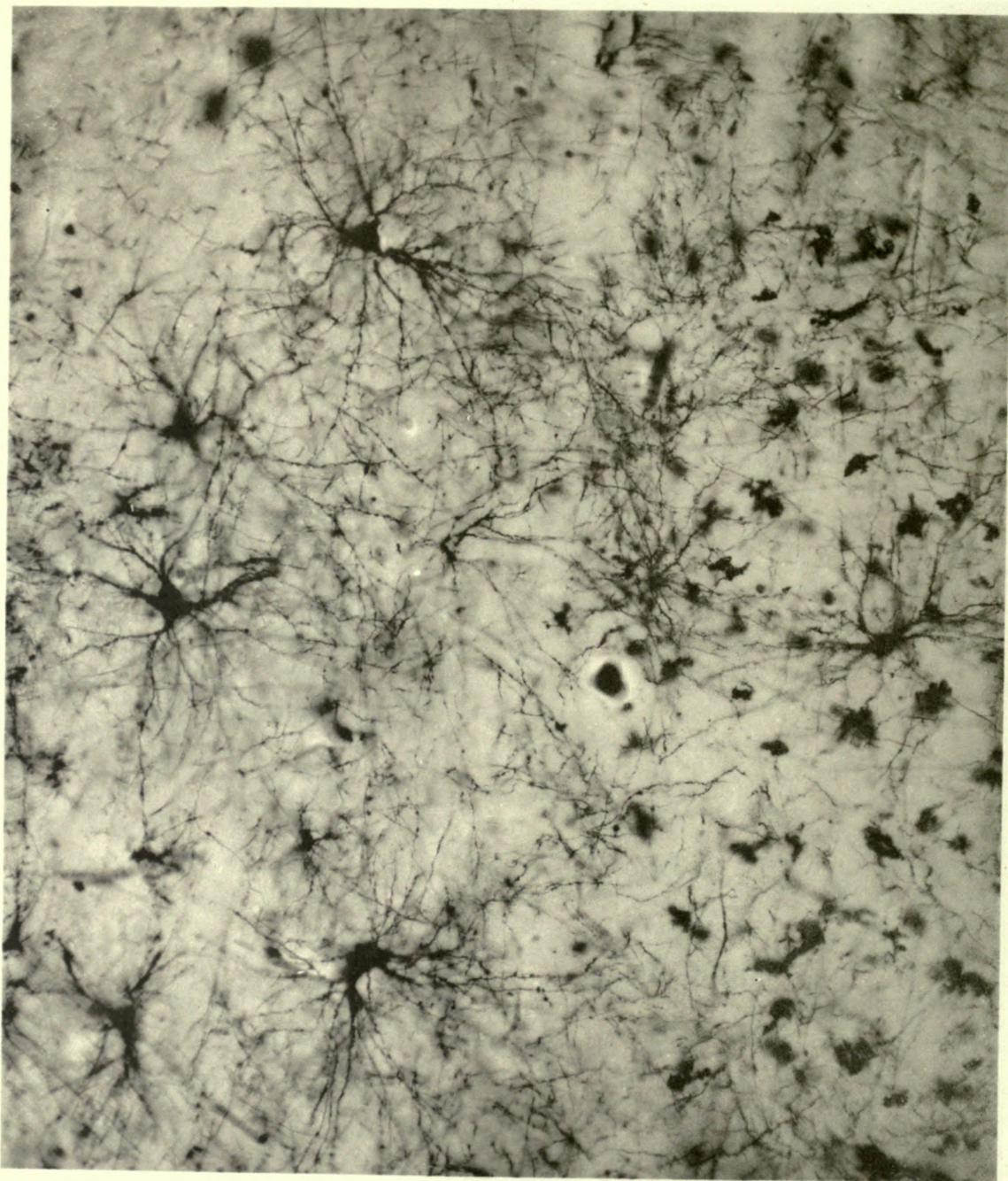DRITES, FROM THE MEDIAN NUCLEUS. X 190 DIAM.

PLATE XXV.

LARGE STELLATE CELLS OF THE OPTIC THALAMUS WITH NUMEROUS DENDRITES. FROM THE LATERAL NUCLEUS.   X 190 DIAM.
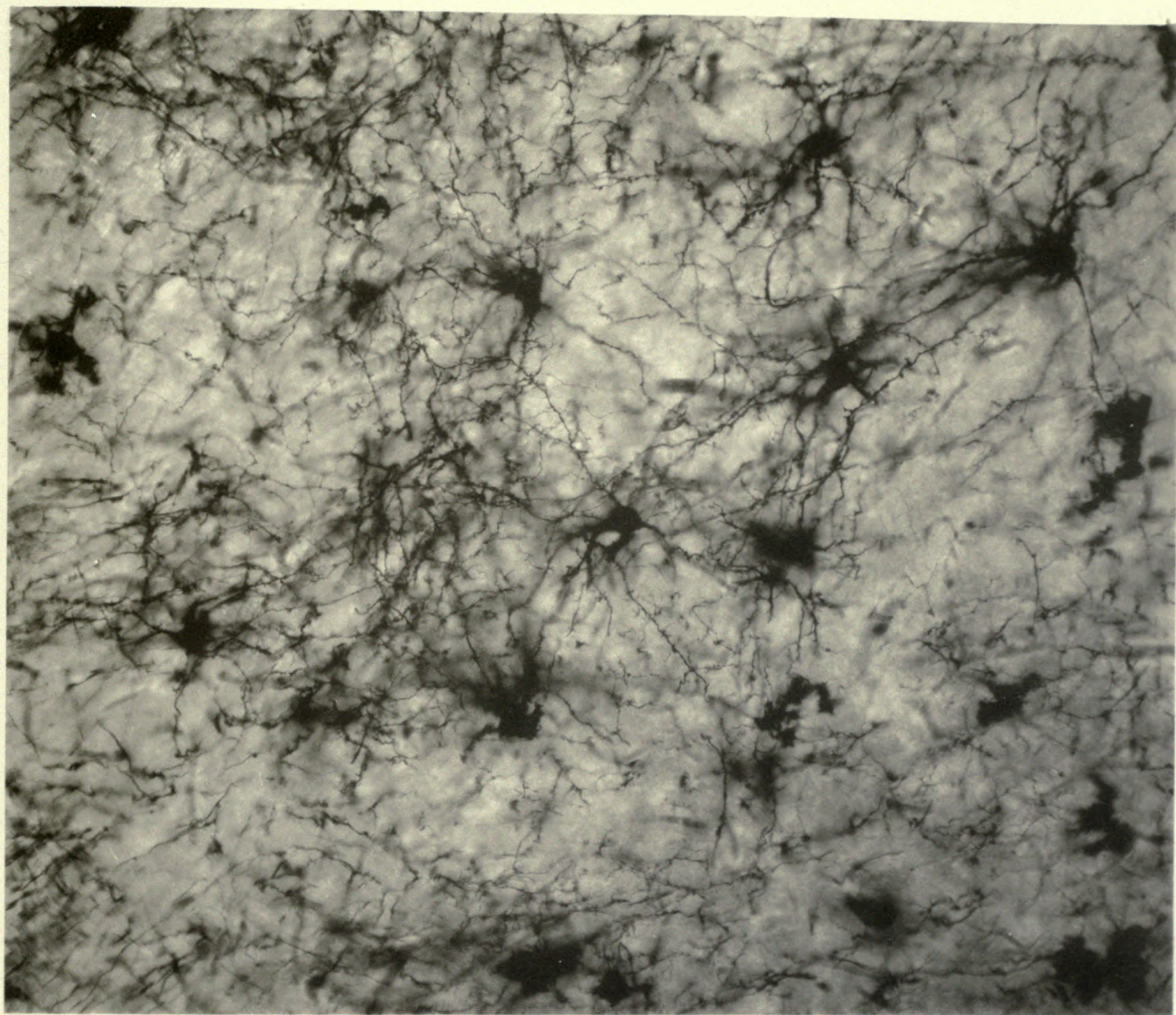
PLATE XXVI.

Plate XXVI. shows a cluster of large stellate cells from the lateral nucleus of the thalamus. They are about 50 μ in diameter. They resemble in appearance the medium-sized cells of the median nucleus, but are distinctly larger. They are to be found scattered irregularly throughout the lateral nucleus; but a special group of these cells appears to be constant in its inner part, near the dorsal part of the median nucleus. These stellate cells are, however, found along the free margin of the thalamus, in the tuberculum anterius and in the pulvinar, and also occasionally single cells are seen in the internal capsule among the fibres. The neuraxon is difficult to follow and may come off on any side of the cell. It takes a very devious course. Marchi affirms that there are to be found both of the Golgi types of cell in the thalamus. It has not been possible for me to confirm this statement, as the difficulties in the way of following the neuraxons for any distance are insuperable.

Plate XXVII. shows a second variety of cell found only in the ventral nucleus of the optic thalamus, and hitherto undescribed. These cells are placed quite regularly at definite distances from one another, so that the nucleus presents a very different appearance under the microscope from other parts of the thalamus, in which irregular distribution of the cells is the rule. These cells are very large, from 50 to 60 μ in diameter. They have a large body, irregular in shape, polygonal as a rule, never fusiform, and from this body numerous dendrites are given off in all directions. These dendrites are very slender in comparison with the size of the cell, but are very long. They appear to take a tortuous course, and branch less freely than the dendrites of the stellate cells. Some of the dendrites are seen to possess the furry surface, which is most marked in the Purkinje cell branches. But there is no uniformity in the direction of these dendrites. The neuraxon, one of which is well shown coming off from the lower side of the cell in the upper right corner of the plate, passes out of the body of the cell on any one of its sides, and gives off few collaterals. There is no uniform direction in the course of the neuraxons of these cells.

LARGE POLYGONAL CELLS OF THE OPTIC THALAMUS WITH NUMEROUS DENDRITES, FROM THE VENTRAL NUCLEUS. X 190 DIAM.
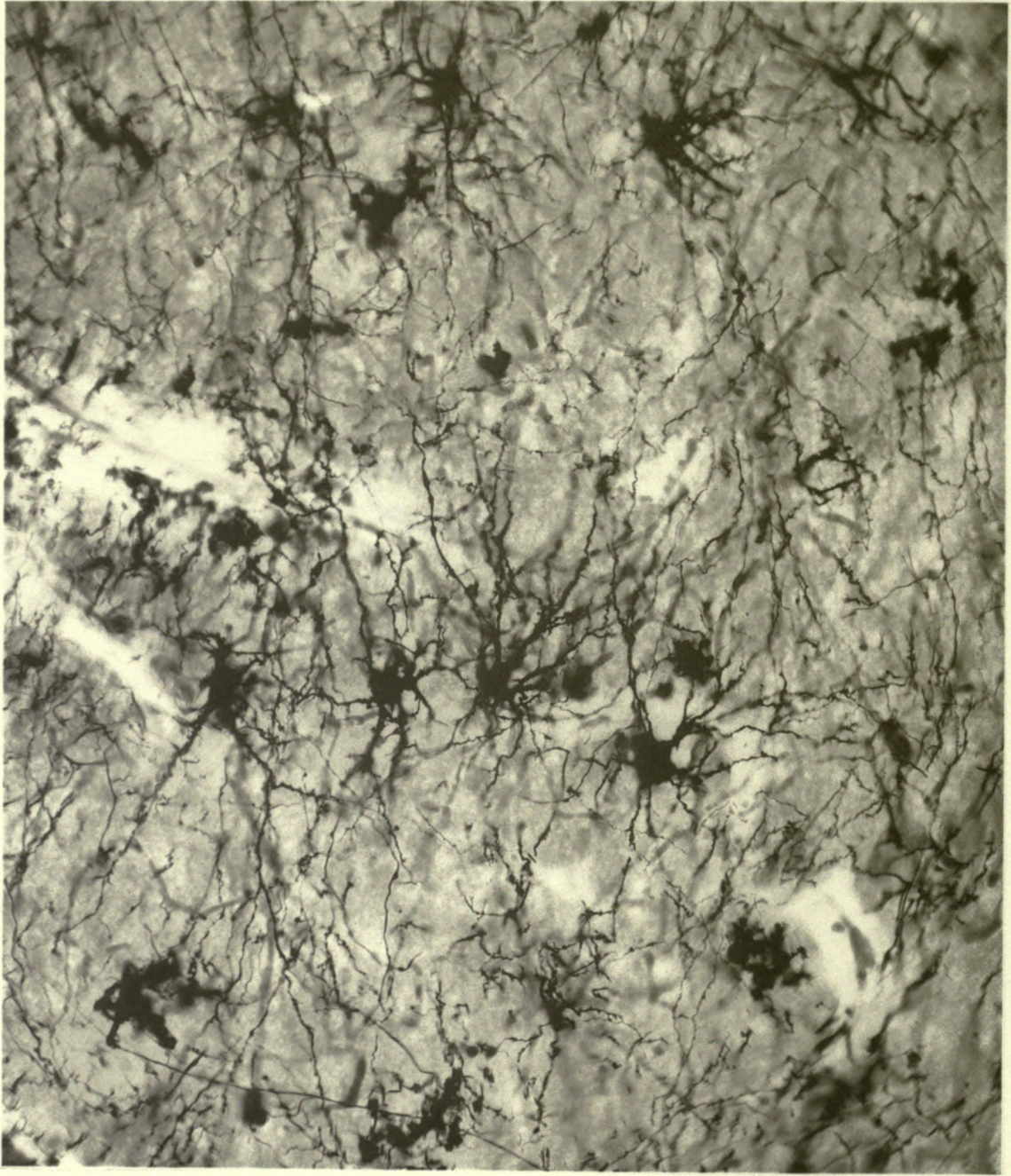
PLATE XXVII.

LARGE POLYGONAL CELLS OF THE OPTIC THALAMUS WITH VERY NUMEROUS DENDRITES FROM
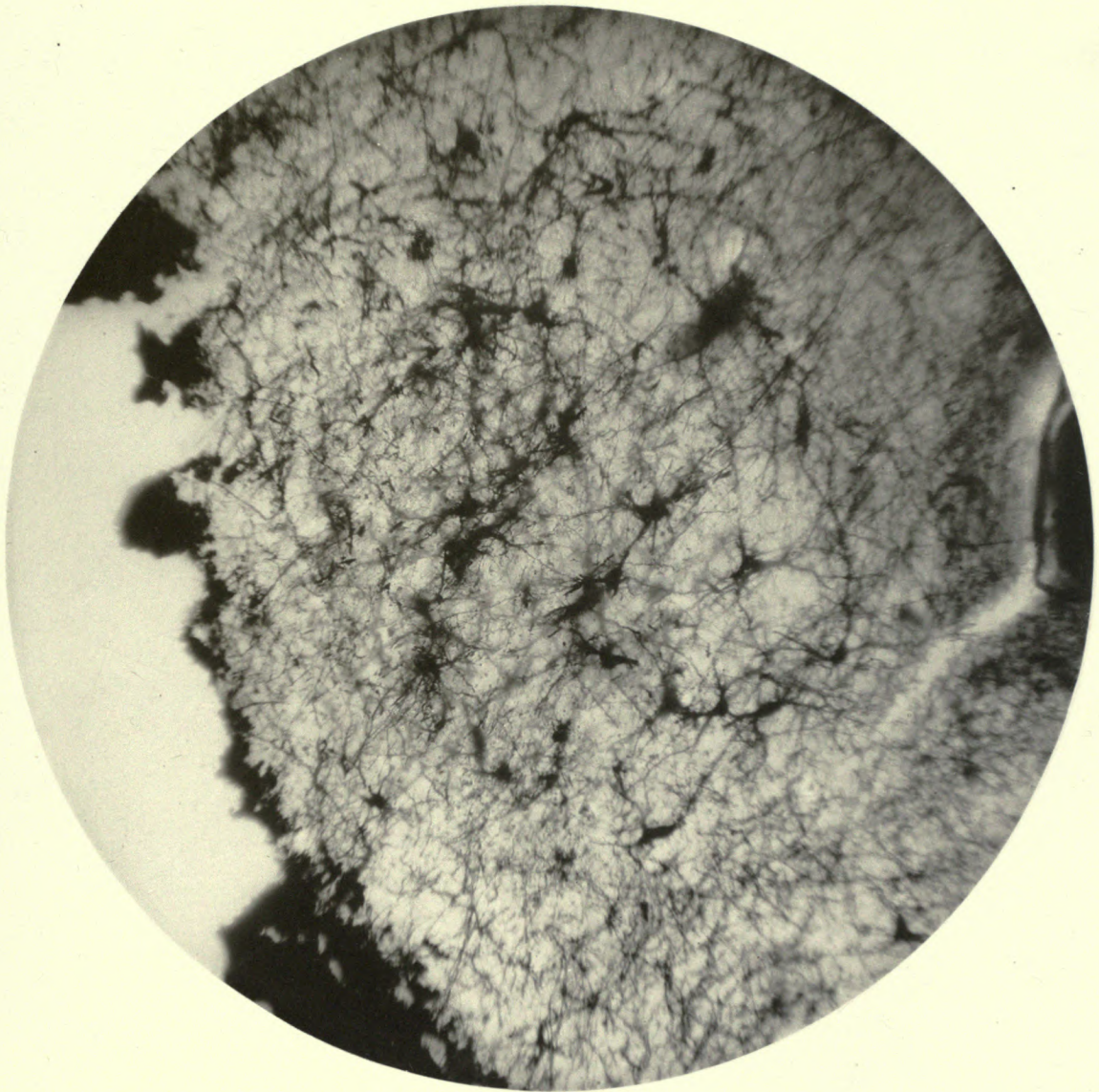THE VENTRAL NUCLEUS. X 190 DIAM.

PLATE XXVIII.

Plate XXVIII. shows the cells of the ventral nucleus of the thalamus. The nucleus is bounded above by a distinct band of nerve fibres, entering the thalamus from the internal capsule and sweeping inward toward the median nucleus. It is bounded on its outer and lower surface by the fibres of the internal capsule. Hence it is more distinct as a separate nucleus than any other of the thalamic masses. It is also distinguished from other nuclei by the size and appearance of its cells, as already described. The cells of Luys' body, which lies not far from this nucleus among the longitudinal bundles of the internal capsule, resemble these cells.

Plate XXIX. shows a group of cells of smaller size than those already shown and chiefly triangular in shape, which is found on the median border of the thalamus in its posterior portions. These cells are not only grouped together, but are scattered along the median surface of the thalamus in a thin layer over a considerable area. The large group is the ganglion habenulæ, shown as a distant hillock (*h*) in Fig. 9, *A*. This ganglion gives rise to a set of fibres which pass backward to the level of the posterior commissure, forming the pillars of the pineal gland. It also gives origin to a band of fibres which passes downward and backward between the red nuclei of the tegmentum to a small mass of gray matter lying between the crura. This band is the fasciculus retroflexus of Meynert. It is shown in Fig. 8.

The majority of the cells of the ganglion are triangular, with three chief dendritic branches, but some are polygonal, with many dendrites. The neuraxon is very fine, and has few, if any, collaterals. The majority of the neuraxons turn downward and probably pass into the fasciculus retroflexus. In the plate the free median border of the thalamus is seen to the left.

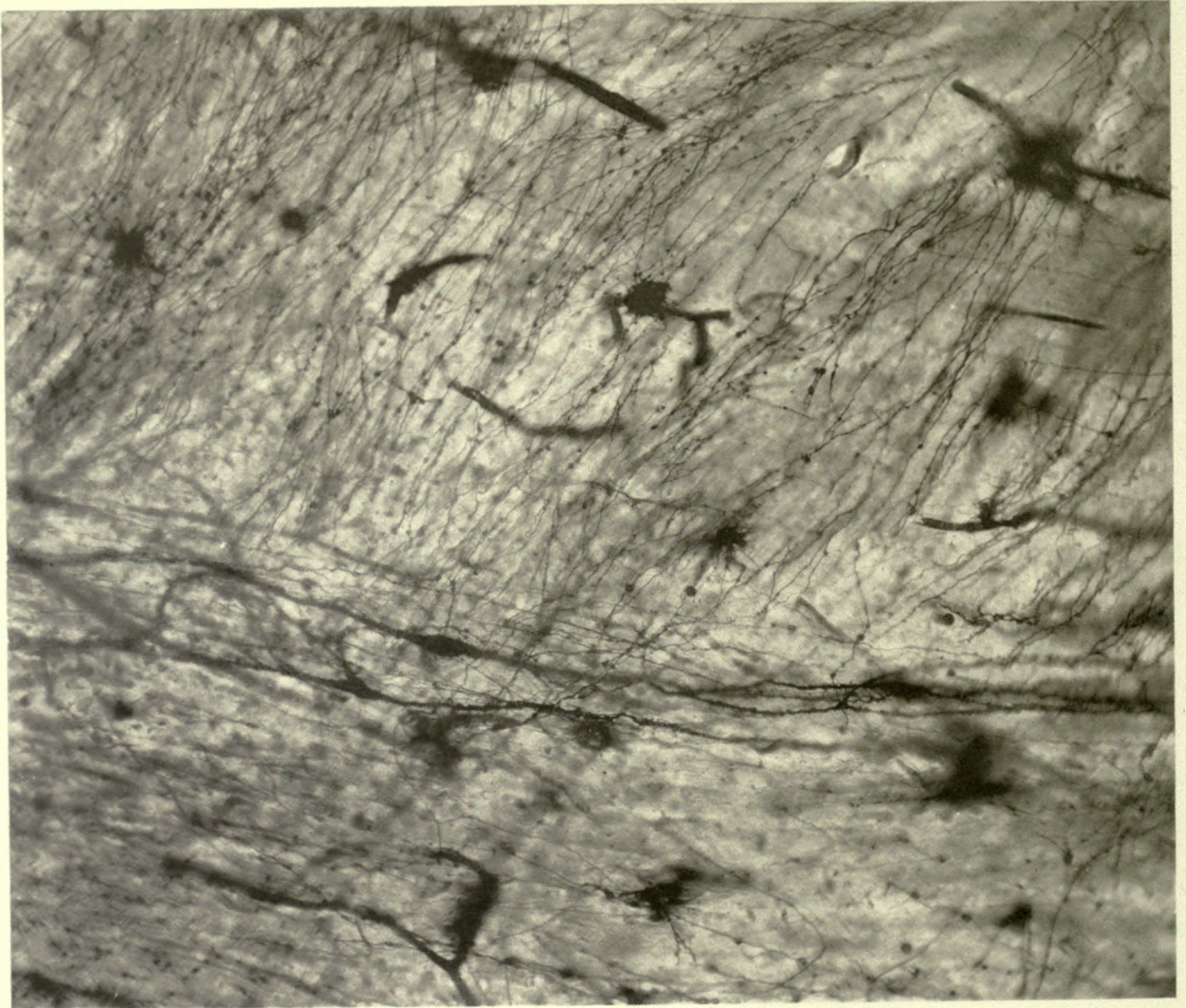SMALL TRIANGULAR CELLS OF THE NUCLEUS HABENULAE OF THE OPTIC THALAMUS.

PLATE XXIX.

SECTION THROUGH THE MARGIN OF THE OPTIC THALAMUS SHOWING THE ENTRANCE OF ITS
FIBRES INTO THE INTERNAL CAPSULE.   TWO FUSIFORM CELLS ARE SEEN WHOSE LONG AXIS IS
PARALLEL WITH THE CAPSULAR FIBRES. THE MAJORITY OF AXIS CYLINDERS APPEAR VARICOSE AND
A FEW ARE SEEN TO GIVE OFF COLLATERALS.   X 190 DIAM.

PLATE XXX.

Plate XXX. shows the outer margin of the optic thalamus adjacent to the internal capsule. The object of the plate is to demonstrate the enormous number of fine neuraxons issuing from the thalamus and entering the internal capsule. The thalamic fibres are shown in the plate as passing from above downward and toward the left. The internal capsule fibres are shown passing across the plate below. Among the latter, two long fusiform cells are seen near the thalamus, with very long branches which subdivide at some distance from the cell. Such cells are seen along the outer side of the thalamus in all sections and even in the laminæ medullares within the thalamus. They form a fourth variety of thalamic cell. The fibres from the thalamus turn in a spiral manner on entering the capsule and become parallel with the fibres of the capsule, but such turning cannot be shown by a photograph, which is necessarily in one plane only.

Von Monakow has proven by experimental researches on animals and by studies in pathology in man that the neurons in the thalamus must be considered as made up of two categories: (1) cells which lie in the thalamus and send out neuraxons which pass to and terminate in the cortex; (2) neuraxons of cortical cells passing into the thalamus and terminating in brush-like expansions about its cells. By means of these two sets of neurons the mutual relation of the nuclei of the thalamus and the cortical areas, already described, are maintained. He believes that the mutual relations of these neurons is secured by the intermediate action of cells of Golgi's second type lying in the optic thalamus. I have not included such cells in the diagram, Fig. 8. There are undoubtedly many other fibres leaving and entering the thalamus to and from the lower levels of the central nervous system, as well as those which enter it from the optic tracts. The latter are clearly connected with the pulvinar of the thalamus and with the corpora geniculata. There is no reason to believe that the other nuclei of the thalamus have any anatomical relation with the optic tracts. The relations known to exist between the optic nerve, pulvinar, and occipital cortex may, however, be taken as indicative of the relation between other parts of the thalamus and other subcortical and cortical structures. These have been shown already in the diagram of the visual tract, Fig. 8.

It is probable that the thalamus is the organ in which many automatic acts are coördinated under the stimuli of various sensory impressions there united and brought into mutual relation. Its exact function is, however, undetermined.
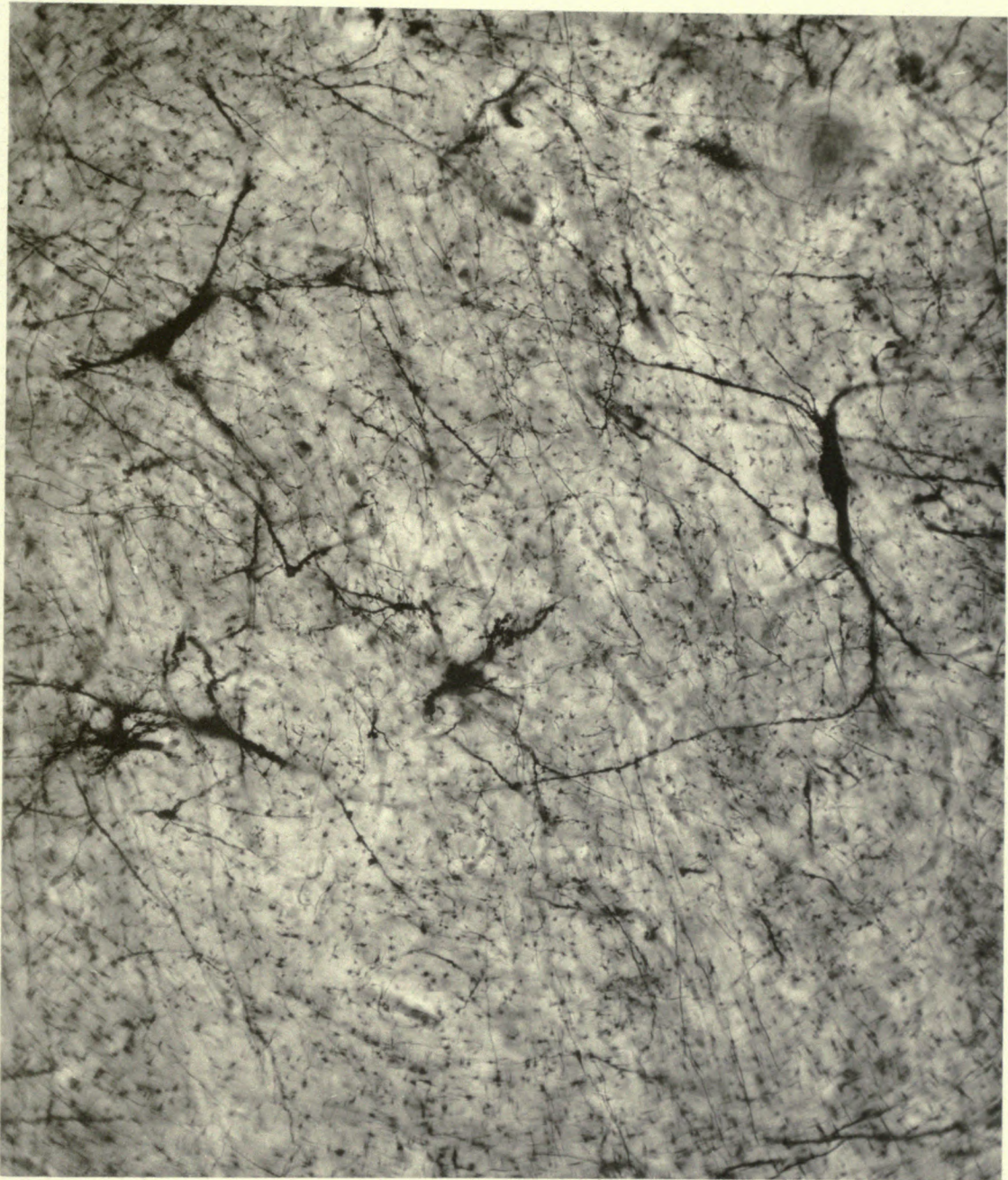
THE CORPUS STRIATUM

THE corpus striatum of each hemisphere, a single mass of gray matter on the base of the brain in its anterior part, is divided above into two parts, the caudate and lenticular nuclei, by the passage downward of the fibres of the internal capsule. The caudate nucleus has a free upper surface forming a part of the floor of the lateral ventricle. The lenticular nucleus is surrounded on all sides by white matter, being bounded externally by the external capsule, internally by the internal capsule, and below by the lenticular loop. It is subdivided into an external body or putamen, a median portion, the lobus intermedius, and an internal portion, the lobus pallidus, by two bands of white fibres coursing through it from the internal capsule to the lenticular loop. These relations are shown in Fig. 9, *B*, on page 52.

Microscopical examination of the caudate and lenticular nuclei shows that they are essentially alike in structure. They are made up of gray substance containing two varieties of cells; very large rectangular cells and very small triangular or polygonal cells. These cells are scattered indifferently through the mass of gray matter and are never collected into groups. Plate XXXI. shows the large variety of cells characteristic of the corpus striatum. They are 70 μ long and 10 μ to 15 μ broad. The body of the cell is long and narrow with a swelling in its middle where the nucleus lies. At the extremities of the cell body dendrites are given off, either one or two in number, and these appear to turn at right angles to the long axis of the cell soon after leaving it. They give off very few branches and have a very long course, being often traceable for a great distance through the gray matter and even into the internal capsule. The neuraxon may arise from the body of the cell, but usually arises from one of its protoplasmic prolongations near the body. It usually turns soon after its origin toward the internal capsule, but does not uniformly arise from the side of the cell toward the capsule. The majority of the neuraxons in the caudate nucleus enter the capsule from its under surface. Those from the lenticular nucleus either pass into the lenticular loop by way of the laminæ, dividing the nucleus into its three parts, or else enter the capsule after traversing the lobus pallidus.

LARGE RECTANGULAR CELLS OF THE CORPUS STRIATUM. THESE CELLS ARE FOUND ONLY
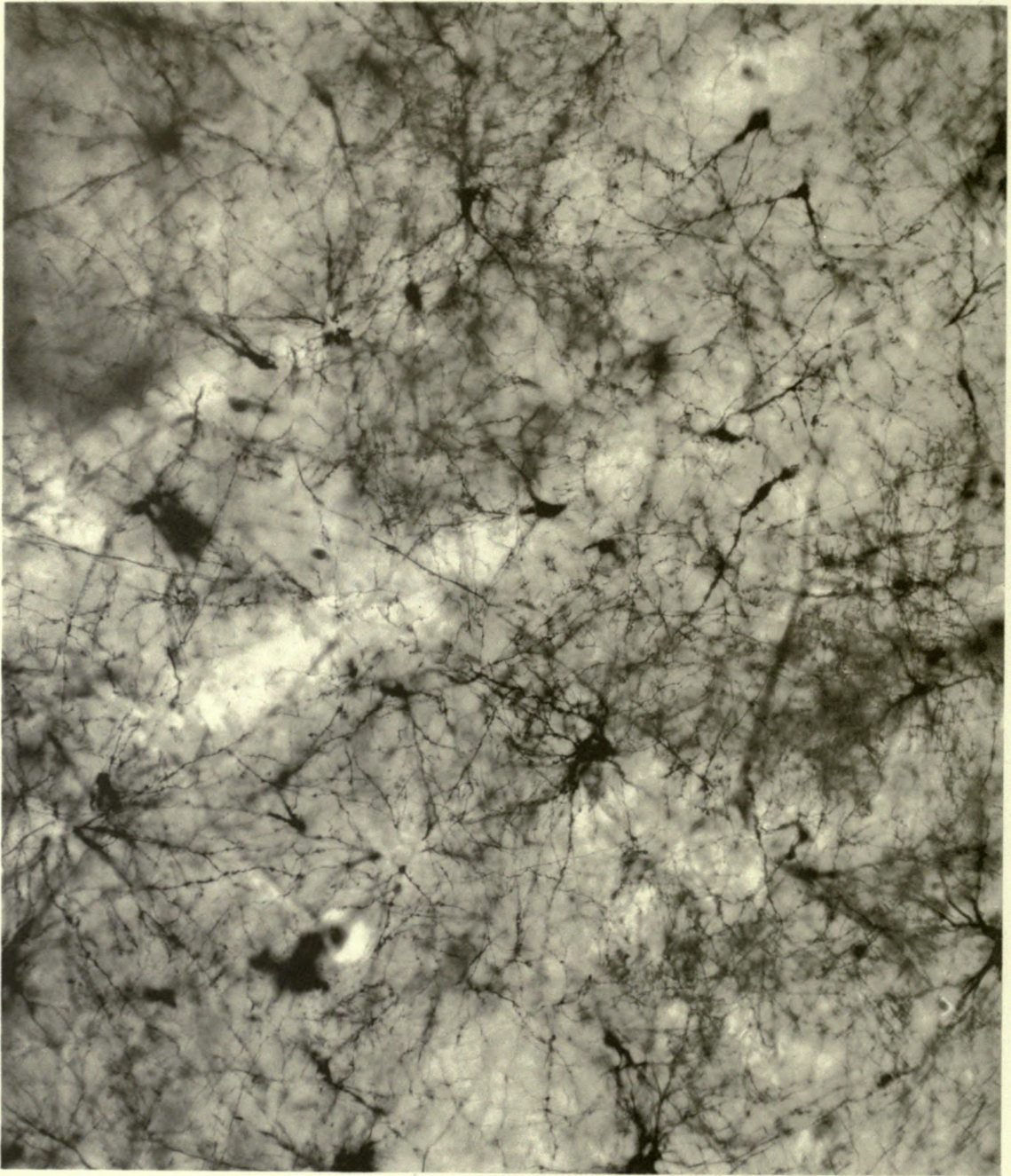IN THIS REGION. X 190 DIAM.

PLATE XXXI.

SMALL TRIANGULAR AND STELLATE CELLS IN THE CORPUS STRIATUM. X 190 DIAM.

PLATE XXXII.

Plate XXXII. shows the second or smaller variety of cells found in the corpus striatum. These may be stellate cells quite like those of the thalamus, of which one is shown in the plate; or they may be very small triangular cells, with protoplasmic prolongations coming off at right angles, or at acute angles to each other. Several such small cells are shown in the plate. The majority of the dendrites of these small cells run in an antero-posterior direction; hence in the section shown, which is a frontal section, they are cut off, and cannot be traced far. They have few branches, and are not long. The neuraxons of these cells come off in all directions, and cannot be followed. It has been asserted by Marchi that cells of both the types of Golgi are present in the corpora striata. It is evident in both plates that a fine plexus of neuraxons is present throughout the gray matter, and numerous collaterals can be seen coming off from these fibres.

No definite relation between the corpus striatum and the cortex has been demonstrated, though Kovalewski[1] believes that fibres enter the outer surface of the putamen from the corona radiata, and external capsule, and end there, establishing such a relation.

The function of these ganglia is undetermined.

[1] Sitzb. d. K. Akad. d. Wissensch. im Wien, Bd. LXXXVI. iii. Abt., December, 1882.
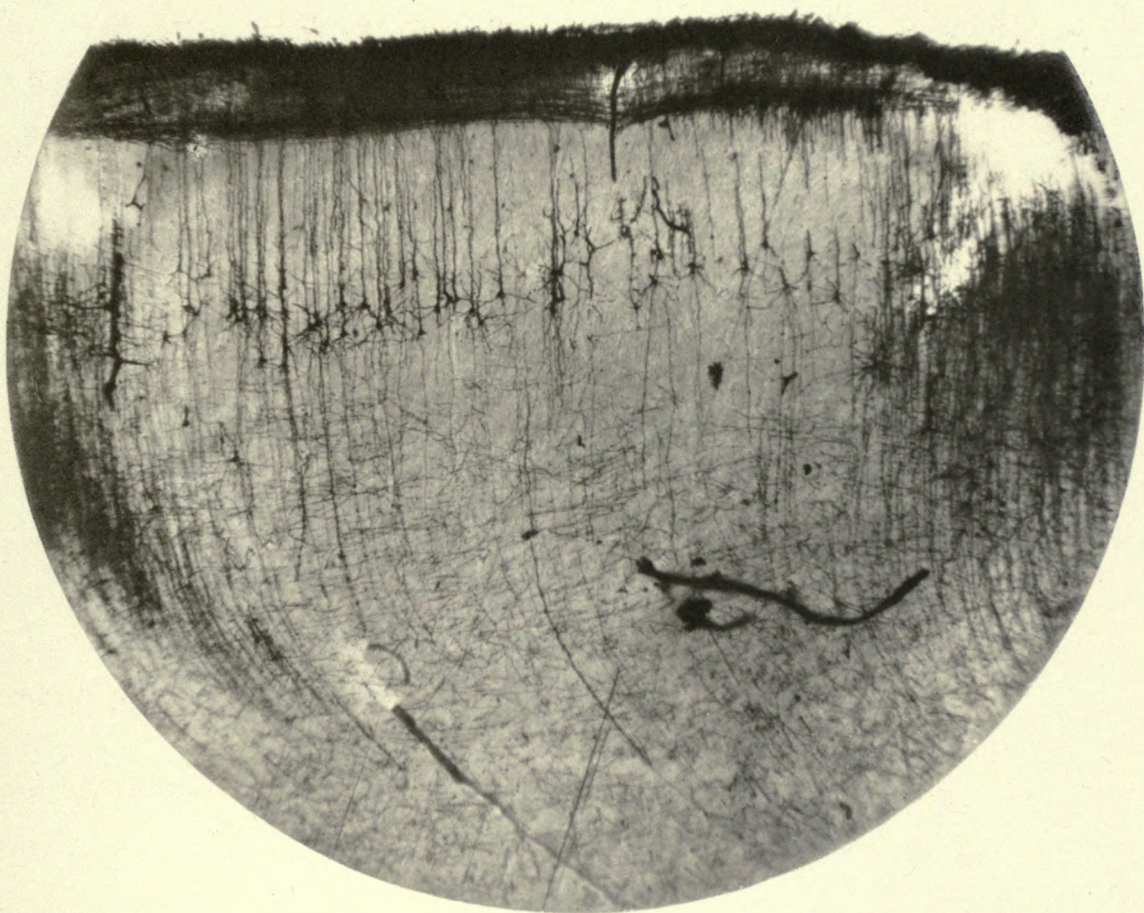
THE CEREBRAL CORTEX

General Topography

PLATES XXXIII. to LIII. show the structure of the cerebral cortex. This is the most intricate portion of the nervous system. It has formed the subject of numerous careful studies, but there remain many points which are still obscure, and there is as yet much uncertainty regarding the arrangement of its cells and the direction of its fibres. The methods of Golgi have, however, been particularly successful in demonstrating the constituent parts of the cortex, in revealing the existence of numerous varieties of cells, in tracing the division and destination of their branches, and in unravelling the tangled mass of fibres which permeate it everywhere. The description here given rests largely upon the study of the facts presented by Golgi, Cajal, and Retzius, and illustrated in the plates.

Plate XXXIII. shows a section through the cortex of the Rolandic region of a human embryo of eight months. It gives a general idea of the topography of the cortex at a period in the development when the structure is simple, and the various layers can be easily distinguished. It is evident that there are several layers in the gray matter. In this plate the superficial layer is so deeply stained that little of its structure can be seen, although some fibres parallel to the surface, so-called tangential fibres, can be made out in the lighter parts. The characteristics of this layer are shown in Plates XXXIV. to XXXVII. Beneath the superficial layer a comparatively clear region is seen having a striated appearance, because traversed by long fibres at right angles to the plane of the surface. These fibres are really the long, slender, upright apical extensions of the pyramidal-shaped cells which form the second and third layers. A careful inspection, however, will show here and there in this clear zone some small cells with little apices extending upward toward the surface. And when the layer of large pyramidal cells is studied, it will be noticed that these cells lie at different levels, a number of smaller ones being nearer to the surface than the very large ones which first catch the eye. A number of deeper lying cells are visible at the right of the plate. There is really no sharp dividing line between the layers of small and large pyramid cells; and although modern authors divide them into two distinct layers, the plates demonstrate that they intermingle. Beneath the layer of cells is another fairly clear zone occupied

SECTION THROUGH A CONVOLUTION OF THE HUMAN BRAIN, FROM AN EIGHT MONTHS EM-
BRYO. THE VARIOUS LAYERS OF THE CORTEX ARE SHOWN AND THE WHITE FIBRES PASSING TO-
GETHER BENEATH THE CORTEX.   X 29 DIAM.

PLATE XXXIII.

chiefly by the basal or axis cylinder processes of the pyramid cells which sweep downward, forming the mass of parallel fibres which make up the white matter under the cortex. But it is quite evident that interlacing with these fibres, and passing at right angles to them, are many other fibres; and although the cells from which they arise are not here shown, it can easily be believed that these cells and fibres form a fourth layer. After these plates have been studied, some statements will be made regarding the arrangement of the cells in different layers in the various regions of the brain.
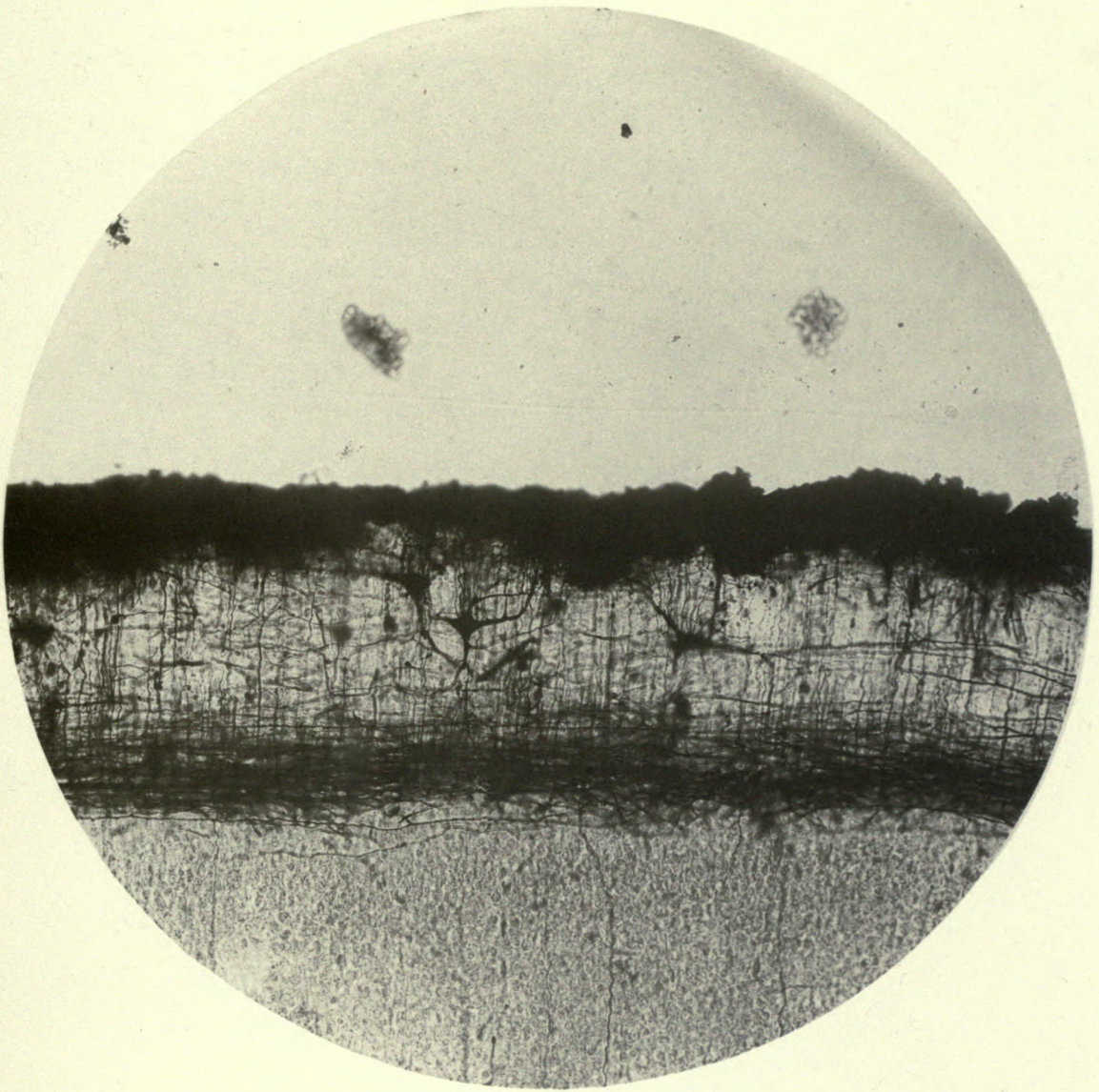
The First, or Superficial Layer

Plates XXXIV. to XXXVII. show the superficial layer of the cortex. This is also known as the molecular layer, from its punctate appearance under the carmine stain and from its supposed lack of nerve cells. The modern methods of staining have demonstrated the existence of a peculiar type of cell in this layer and also the existence of a fine interlacing mass of fibres. These cells having been first described by Cajal are now known by his name; but Retzius[1] has studied them more thoroughly in the human brain, and to him we owe most of our knowledge of these structures. There are several varieties of Cajal cells, all of which are shown in the plates.

Plate XXXIV. shows two of these cells, one fusiform, one triangular. The fusiform cell has an oval body, whose long axis is parallel to the surface of the convolution; and two long protoplasmic processes, called stalks by Cajal, which pass out nearly straight in the horizontal plane. These stalks, whose surface is smooth and not covered with gemmules, give off at right angles numerous fine filamentous fibres. These appear to extend vertically toward the surface, and at their ends little knob-like terminations are often seen. They sometimes divide or give off fine ramifications, which in turn become horizontal in their course. These fibres do not leave the surface layer of the convolution. The end of the stalk terminates in a fine fibre, which is very long, and extends a great length horizontally through this layer. The second cell in the plate is a rectangular, diamond-shaped cell. From this cell the stalks come off at right angles to each other, two being horizontal, two being vertical. From both horizontal stalks fine fibres arise, which take a vertical course, and the right-hand stalk finally turns upward. From the lower pointed process of the cell a neuraxon comes off which gives off a collateral, then divides and becomes a tangential, fibre. This is the course taken by the neuraxons of all these Cajal cells, as has been clearly demonstrated by Retzius. They do not leave the superficial layer, but become tangential fibres. The plate shows the large number of tangential fibres. These appear somewhat thicker than in the subsequent plates, owing to a difference in the photographic method adopted.

Plate XXXV. shows a large triangular Cajal cell with two long stalks, both giving off numerous fine vertical branches which pass upward to the surface of the cortex. One of the branches becomes a horizontal fibre and can be traced for some distance. The neuraxon is not shown.

[1] Retzius, Biologische Untersuchungen, Bd. III.; 1894.
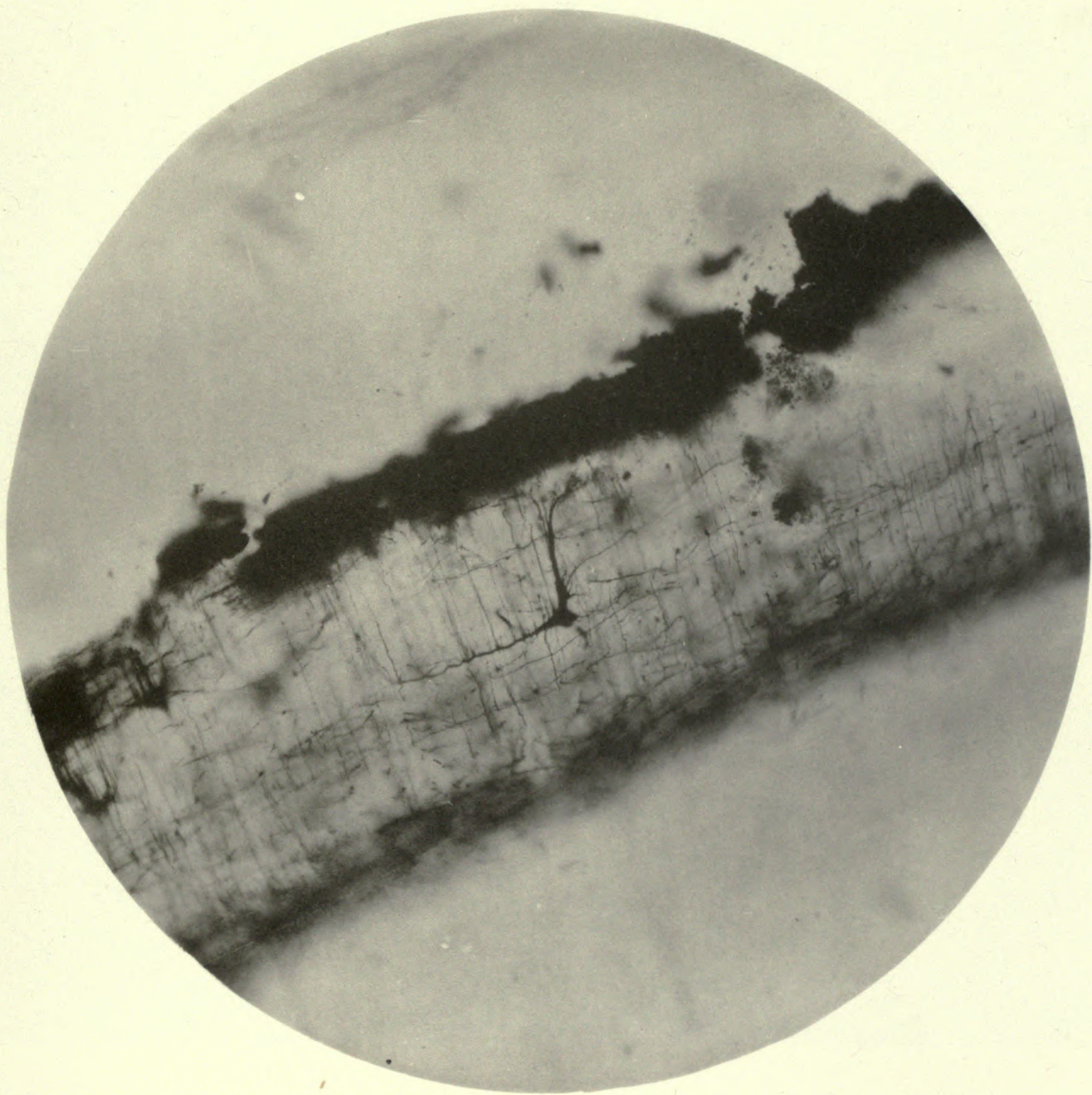
THE SUPERFICIAL LAYER OF THE CEREBRAL CORTEX OF A HUMAN EMBRYO SHOWING CAJAL
CELLS, TANGENTIAL FIBRES, AND FINE INTERLACING VERTICAL FIBRES.   X 190 DIAM.
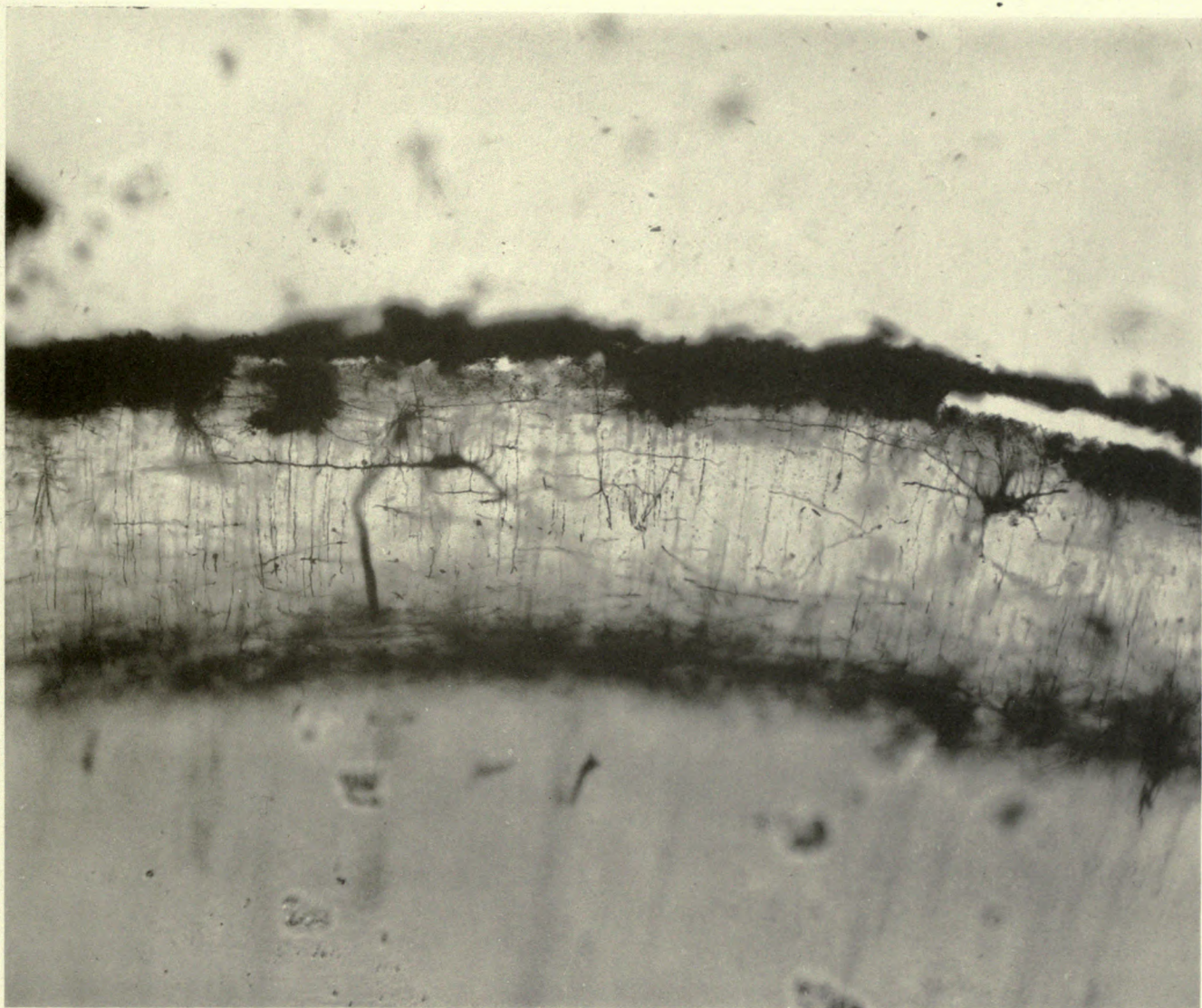

PLATE XXXIV.

THE SUPERFICIAL LAYER OF THE CEREBRAL CORTEX OF AN EIGHT MONTHS HUMAN EMBRYO,
SHOWING TRIANGULAR CAJAL CELL WITH ITS NUMEROUS SECONDARY BRANCHES.   X 190 DIAM.

PLATE XXXV.

THE SUPERFICIAL LAYER OF THE CEREBRAL CORTEX OF AN EIGHT MONTHS HUMAN EMBRYO,
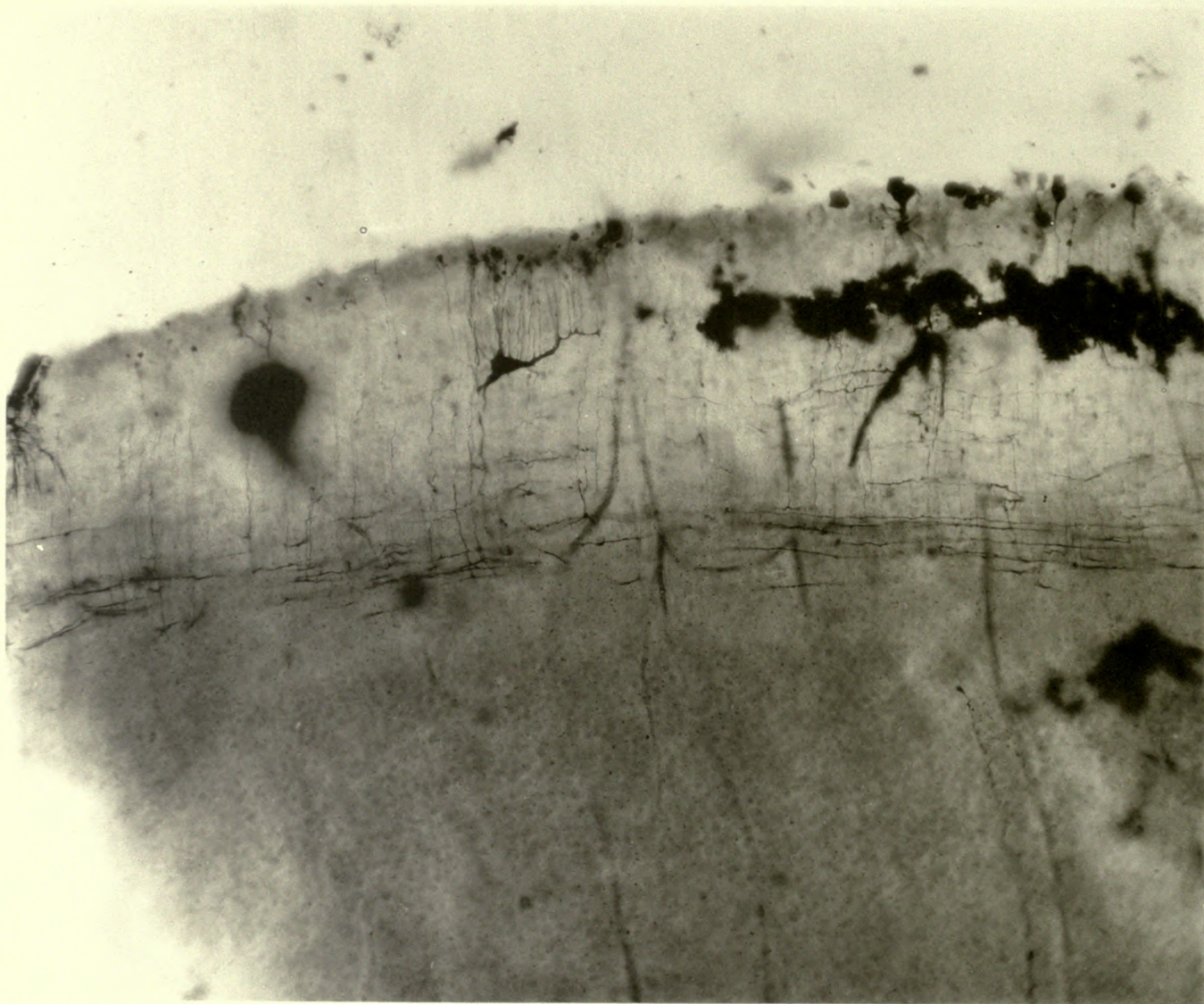SHOWING TWO CAJAL CELLS, ONE FUSIFORM, THE OTHER POLYGONAL.   X 190 DIAM.

PLATE XXXVI.

THE SUPERFICIAL LAYER OF THE CORTEX SHOWING TRIANGULAR CAJAL CELL WITH VERTI-
CAL BRANCHES TERMINATING IN KNOBS. ALSO DEEP TANGENTIAL FIBRES WITH THEIR COLLATER-
ALS.   X 190 DIAM.

PLATE XXXVII.

Plate XXXVI. shows a fusiform cell (*a*[1]) and a polygonal cell (*c*) of the Cajal type in the superficial layer of the cortex. The polygonal cell has several dendrites coming off in various directions and dividing into smaller branches, which diverge. It also has a single neuraxon, very small in diameter, which passes downward into the surface layer and becomes horizontal and gives off collaterals, which also take a horizontal course. These fibres never turn downward to enter the deeper layers. These cells differ in all respects from glia cells, which Golgi has shown to exist in large numbers in this layer.

In all the plates it is evident that there are numerous horizontal fibres in this superficial layer. These are well marked in its deepest portion, and are shown with great distinctness in Plate XXXVII. Into the surface layer there are seen to pass (in Plates XXXVIII. and XLII.) the termination of the apical processes of the pyramidal cells. These have the typical dendrite appearance, being covered with granules, and branching and dividing as they ascend. These dendrites appear to end in free extremities in the superficial layer, there coming into contact with the nerve fibres already described.

Plate XXXVII. shows the triangular variety of Cajal cells (*b*). It also shows the fine interlacing fibres of this layer. The origin of some of these fibres has already been described. There are others which require to be noticed. It has already been stated that the neuraxons ascending to the cortex from the spinal cord, the medulla, the cerebellum, and the basal ganglia terminate in fine brush-like expansions in the cortex. It is in this layer of the cortex that many of these terminal brushes lie. Hence this layer of the cortex certainly receives impulses of many kinds from various parts of the lower nervous centres. It also receives impulses from other regions of the cortex by means of fibres whose terminal expansions have been traced to this layer. Thus the fibres of association from adjacent or distant pyramidal cells end here, as do also many of the collateral fibres coming off from the neuraxons of pyramidal cells in the layer just beneath the superficial layer, and also the neuraxons of certain cells which pass directly to this layer; viz. the Martinotti cells.

If, as Cajal and Van Gehuchten believe, it is the function of the branches of the apical processes of the pyramidal cells of the second and third layers of the cortex to collect impulses and convey them to their cells, it is evident that in the superficial layer of the cortex they can receive such impulses from the most diverse and far separated parts of the central nervous system.

[1] These letters refer to the cells shown in the diagram Fig. 10 on p. 72.

F

The Second Layer, or Layer of Small Pyramidal Cells

Plate XXXVIII. shows the second layer of the cortex or the layer of small pyramidal cells; and Plates XXXIX. and XL. demonstrate the characteristic features of the cells of this layer.   In Plate XXXVIII. the surface layer is seen, but its cells and fibres, excepting a few deep tangential fibres, are not shown.   Just beneath these deep tangential fibres a number of small pyramid cells (*d*) are evident with their short apical processes, really a part of the body of the cell, running up toward the superficial layer.   The size of these cells is from $10\,\mu$ to $12\,\mu$.   In one or two cases the apical process can be seen to bifurcate, and its two branches can be seen to diverge and end in the superficial layer.   Other apical processes coming up from cells lying more deeply, and not shown, can also be seen to take the same course.   The small pyramid cells are seen to have a few dendrites coming off from their basal corners and a true neuraxon coming from the base which can be followed for some distance downward, and in some cases can be seen to give off collaterals.   The majority of the dark broad black lines in this plate are capillary blood-vessels.

In the lower part of the plate the dense mass of nerve fibres interlacing and running in all directions is noticeable.   All through this layer it is evident that fine neuraxons as well as apical projections of deeper cells are making their way toward the surface layer, many of them giving off collaterals in their course.

Plate XXXIX. shows this second layer under a higher power of magnification and brings out the structure and appearance of a few of its cells and the enormous mass of its fibres. Plate XL. shows the characteristics of its cells alone.

The cells have a triangular shape with narrow base and long apex (*e*).   The body gives off a few branches which pass outward, usually downward, from the two basal corners of the cell.   These have the characteristic features of dendrites, tapering as they pass on, having an irregular surface, giving off a few branches at an acute angle, which branches in turn divide and give off secondary branches.   The general direction of these dendrites is diagonal to the vertical fibres of the layer.   The neuraxon also comes off from the base of the cell, but rarely from a corner, usually in the middle.   It differs from the dendrite in being smooth, fine, of uniform calibre, and giving off its finer collaterals at right angles to its course.   Cajal and Golgi believe that many of the collaterals turn in their course and ascend through the second layer to the superficial layer.   It is evident in the plate that this layer
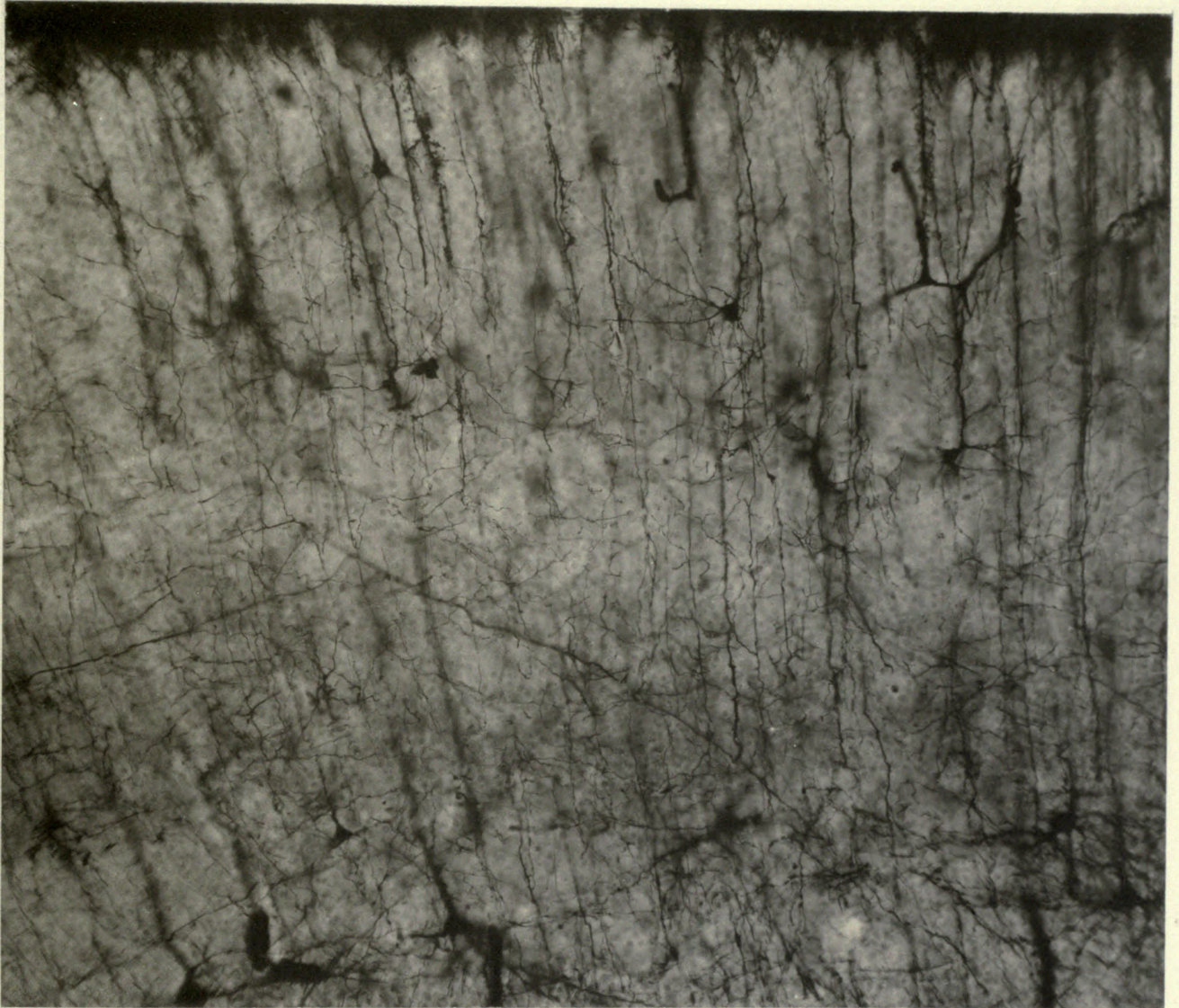
THE SECOND LAYER OF THE CEREBRAL CORTEX OR LAYER OF SMALL PYRAMID CELLS. THE
STRIATED APPEARANCE OF THIS LAYER IS DUE TO THE LARGE NUMBER OF FIBRES COMING UP
FROM THE THIRD LAYER. THE BIFURCATION OF THE APICAL PROCESSES OF THE PYRAMID CELLS
BEFORE ENTERING THE SUPERFICIAL LAYER IS WELL SHOWN, VERY SMALL PYRAMID CELLS WITH
NUMEROUS DENDRITES ARE SEEN AT DIFFERENT PORTIONS OF THIS LAYER.   X 80 DIAM.

PLATE XXXVIII.

THE SECOND LAYER OR LAYER OF SMALL PYRAMIDAL CELLS OF THE HUMAN CORTEX, SEV-
ERAL SMALL CELLS AND VERTICAL AXIS CYLINDERS PASSING THROUGH THIS LAYER ARE SHOWN.
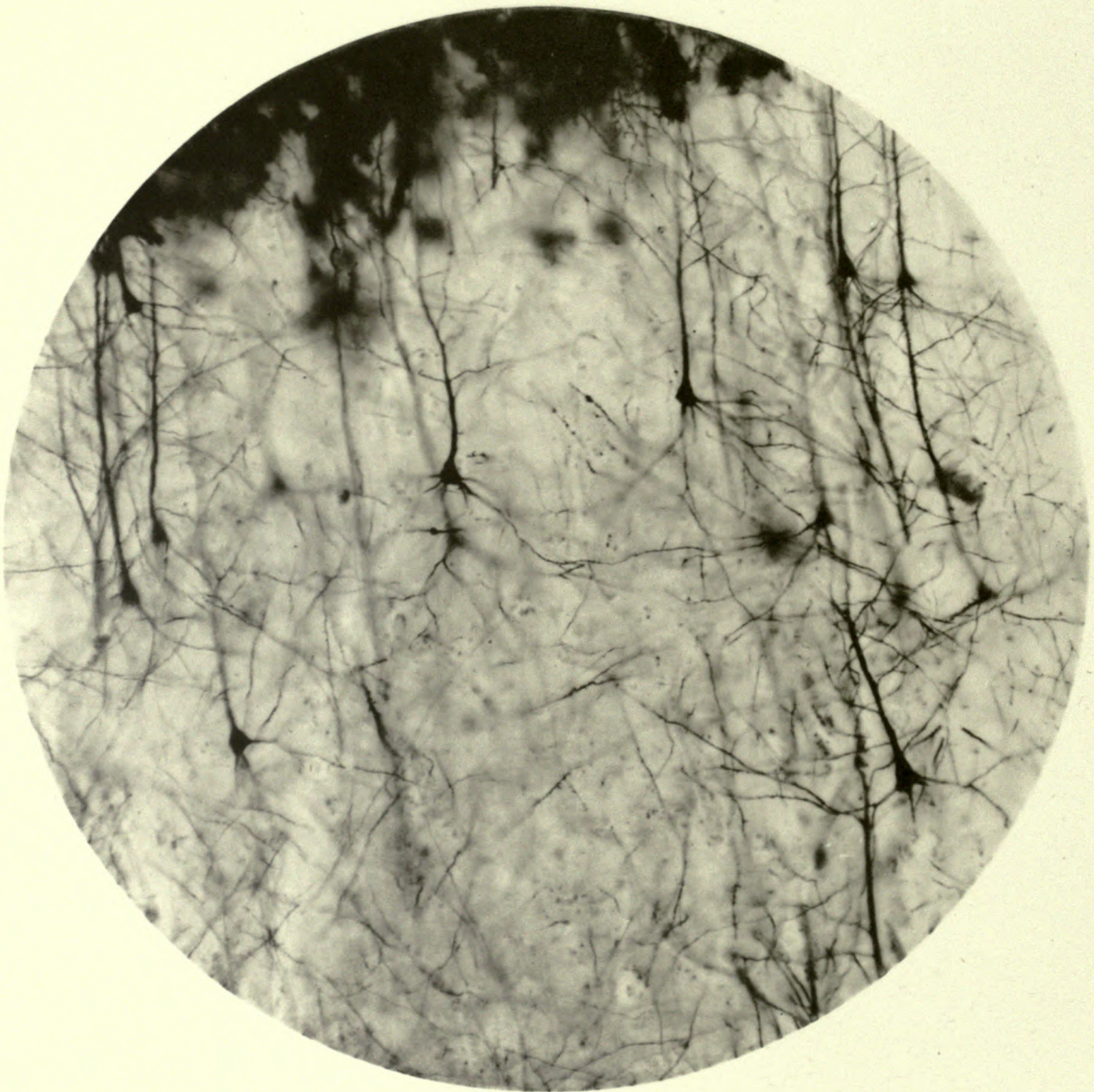X 190 DIAM.

PLATE XXXIX.

PYRAMIDAL CELLS OF THE ADULT HUMAN CEREBRAL CORTEX. THE SHAPE OF THESE CELLS
THE LONG APICAL PROCESS PASSING UPWARD TO THE SUPERFICIAL LAYER, AND THE NUMEROUS
SHORT BASAL DENDRITES ARE SHOWN.   X 190 DIAM.

PLATE XL.

contains many fine neuraxons whose course can be traced to the surface layer though their origin is not seen in the plate. They present a very much finer appearance than the apical processes of the cell near to which they lie.

Plate XL. shows the small pyramidal cells (*f*) of the second cortical layer. These are more distinctly triangular than those shown in Plate XXXIX., and have longer apical processes as they lie at a deeper level. The number of branches from the apical process is larger.

The apical process or stalk of the pyramidal cell is for some distance almost as large as the cell body, and it is many times as long, but gradually becomes narrower and lies straight, and finally divides like a dendrite into branches. In its ascent toward the surface it constantly gives off branches which pursue the same direction or which turn upward soon after passing away from the stalk. In Plate XL. such branches of the apical process are very clearly seen. As the apical process becomes more slender, it often appears to present a varicose appearance, and such varicosities are also seen in its branches.

The Third Layer, or Layer of Large Pyramidal Cells

Plate XLI. gives a general view of the second and third layers of the cortex, or the layers of pyramidal cells. These two layers are only to be distinguished from one another by the size of their cells, the deeper cells being much larger and reaching from 15 μ to 40 μ in diameter. There is no actual boundary between the two layers, and Cajal prefers to consider the two as one. In fact, the cells are small, intermediate, and large, as they lie deeper. Their apical processes or stalks reach up to the superficial layer. The cells are seen to lie at various levels, yet they are so nearly together as to make quite a distinct stratification of the cortex. The characteristics of the cells in the deep or third layer are the great size of the cells, the length of their apical process, and the greater number of the vertical fibres which give this layer a striated appearance. The numerous dendrites of the cells, running out from their bases, and also the neuraxons with collaterals, can be seen in the plate. The special features of this layer are seen to better advantage in the plates which follow.

Plate XLII. shows very clearly a group of intermediate-sized pyramidal cells in a human embryo of eight months.

The cells of the second layer did not stain, hence the course of the apical process can be traced to the superficial layer.
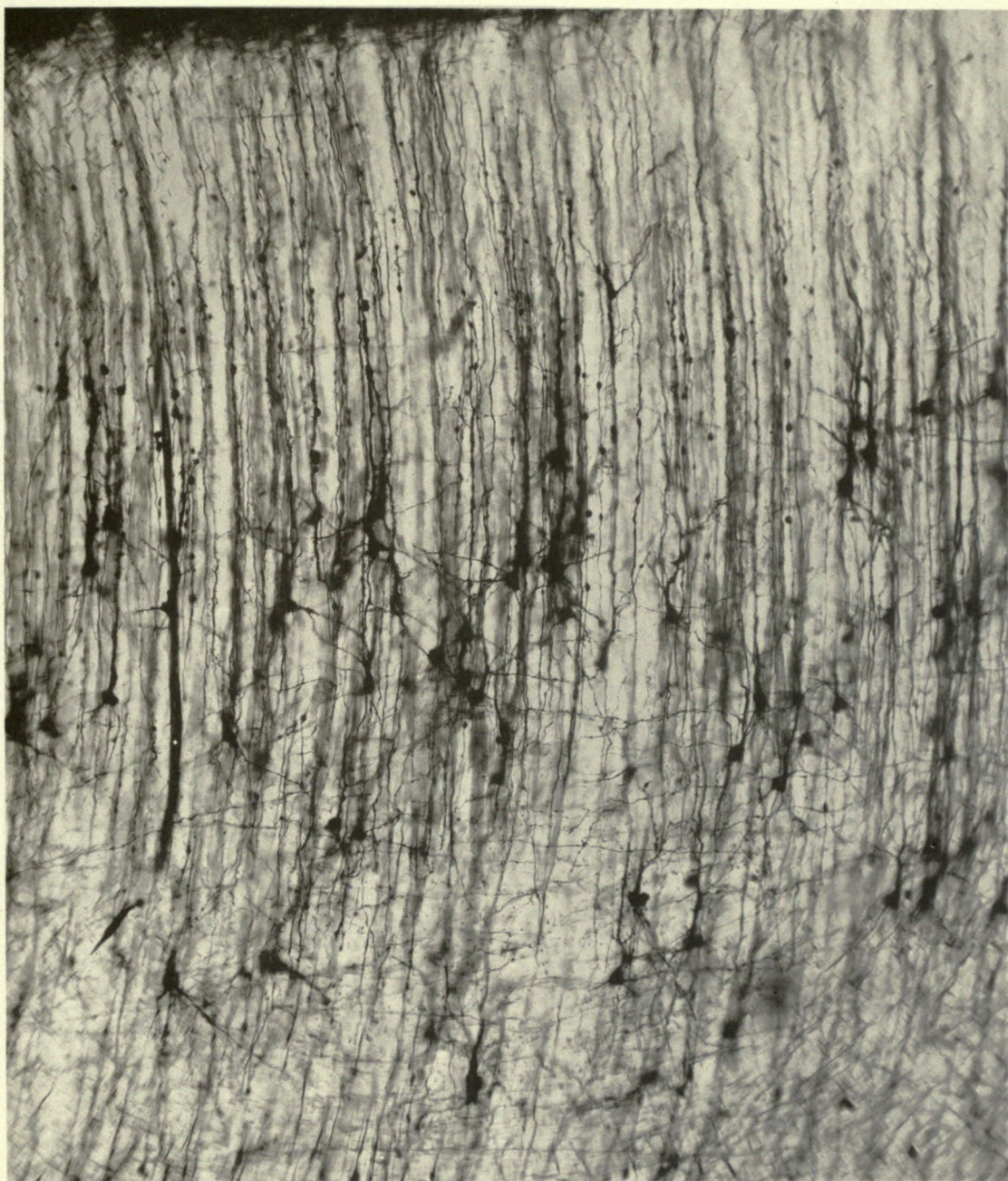
The characteristic triangular appearance of these cells is to be noticed; their dendrites coming off at the corners and subdividing; their long apical projection running far up into the second layer, giving off branches as it ascends, and finally splitting up into two parts, which diverge and enter the superficial layer of tangential fibres; and lastly, their axis cylinder process, coming out of the base, passing downward and giving off one or two collaterals in its course.

It is quite evident that the apex projection has a rough surface covered by gemmules or little spike-like or thorn-like excrescences. These appear to be better marked on this process than on the other protoplasmic processes, though they can be seen on them as well. On several of the apical processes, extending through the plate, varicosities are seen. Andriezen[1] is inclined to attach a pathological significance to these, but Berkley[2] considers them as normal. Their significance is not known. In this plate and in Plates XLIII. and XLVI. a few

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[1] W. L. Andriezen, On Some of the Newer Aspects of the Pathology of Insanity. Brain, Vol. XVII., p. 548; 1894.

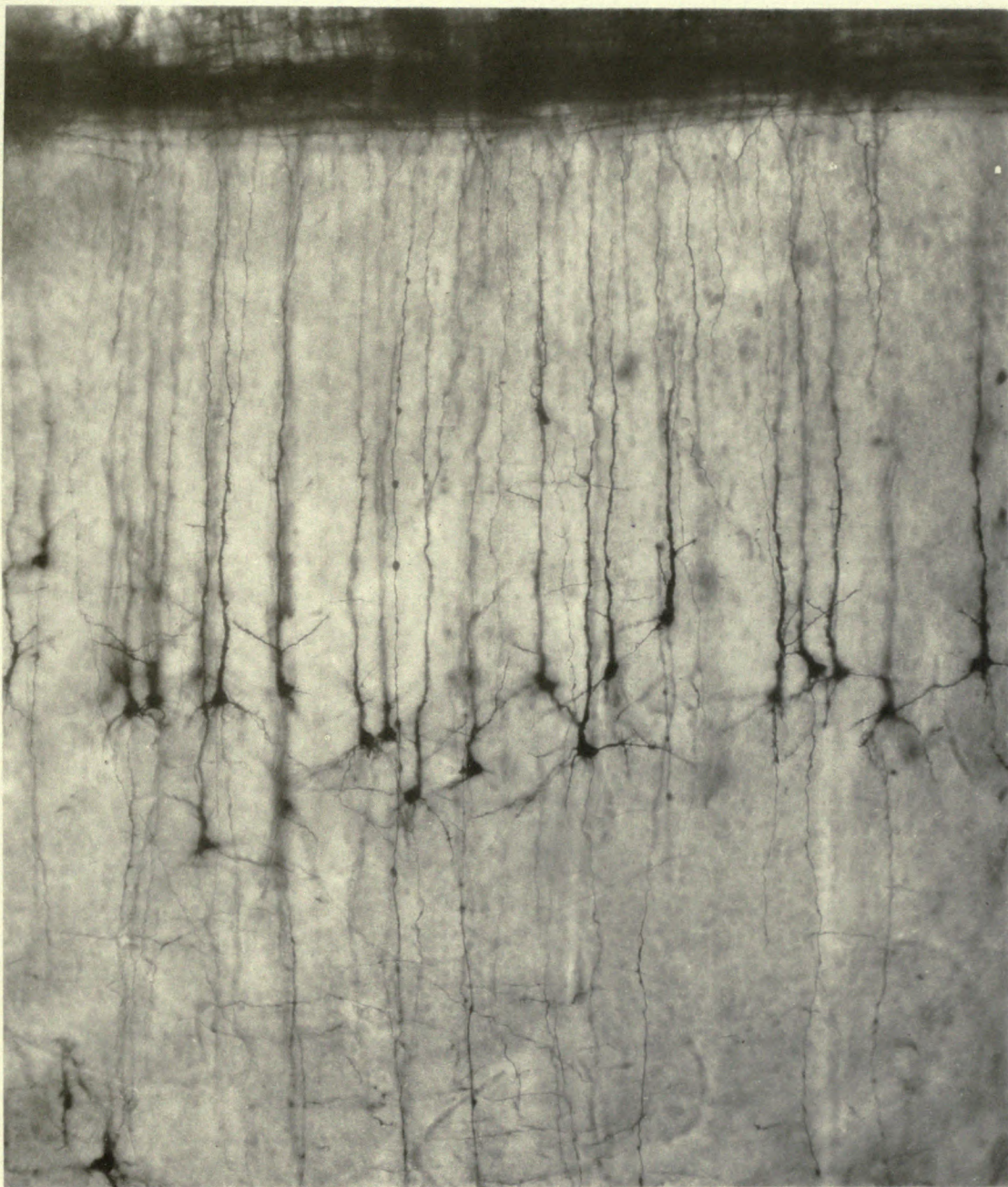[2] H. J. Berkley, A Theory of the Causation of Permanent Dementia. The Medical News; Nov. 9, 1895.

SECTION THROUGH THE SECOND AND THIRD LAYERS OF THE HUMAN CORTEX SHOWING BOTH
SMALL AND LARGE PYRAMIDAL CELLS LYING BETWEEN NUMEROUS VERTICAL FIBRES· X 190 DIAM.

PLATE XLI.

PYRAMIDAL CELLS OF THE CEREBRAL CORTEX, EIGHT MONTHS HUMAN EMBRYO. THE LONG APICAL PROCESS PASSING UPWARD TO THE SUPERFICIAL LAYER, THE NUMEROUS SHORT BASAL PROCESSES AND THE NEURAXON COMING OUT OF THE BASE ARE SHOWN IN THIS SECTION; IT IS POSSIBLE TO SEE COLLATERAL BRANCHES COMING OFF FROM THE NEURAXON. X 190 DIAM.

PLATE XLII.

PYRAMIDAL CELLS OF THE CEREBRAL CORTEX, EIGHT MONTHS HUMAN EMBRYO. THE SHAPE OF THESE CELLS, THE LONG APICAL PROCESS PASSING UPWARD TO THE SUPERFICIAL LAYER, THE NUMEROUS SHORT DENDRITES AND THE NEURAXON WITH ITS COLLATERALS ARE SHOWN IN THIS SECTION.   X 190 DIAM.
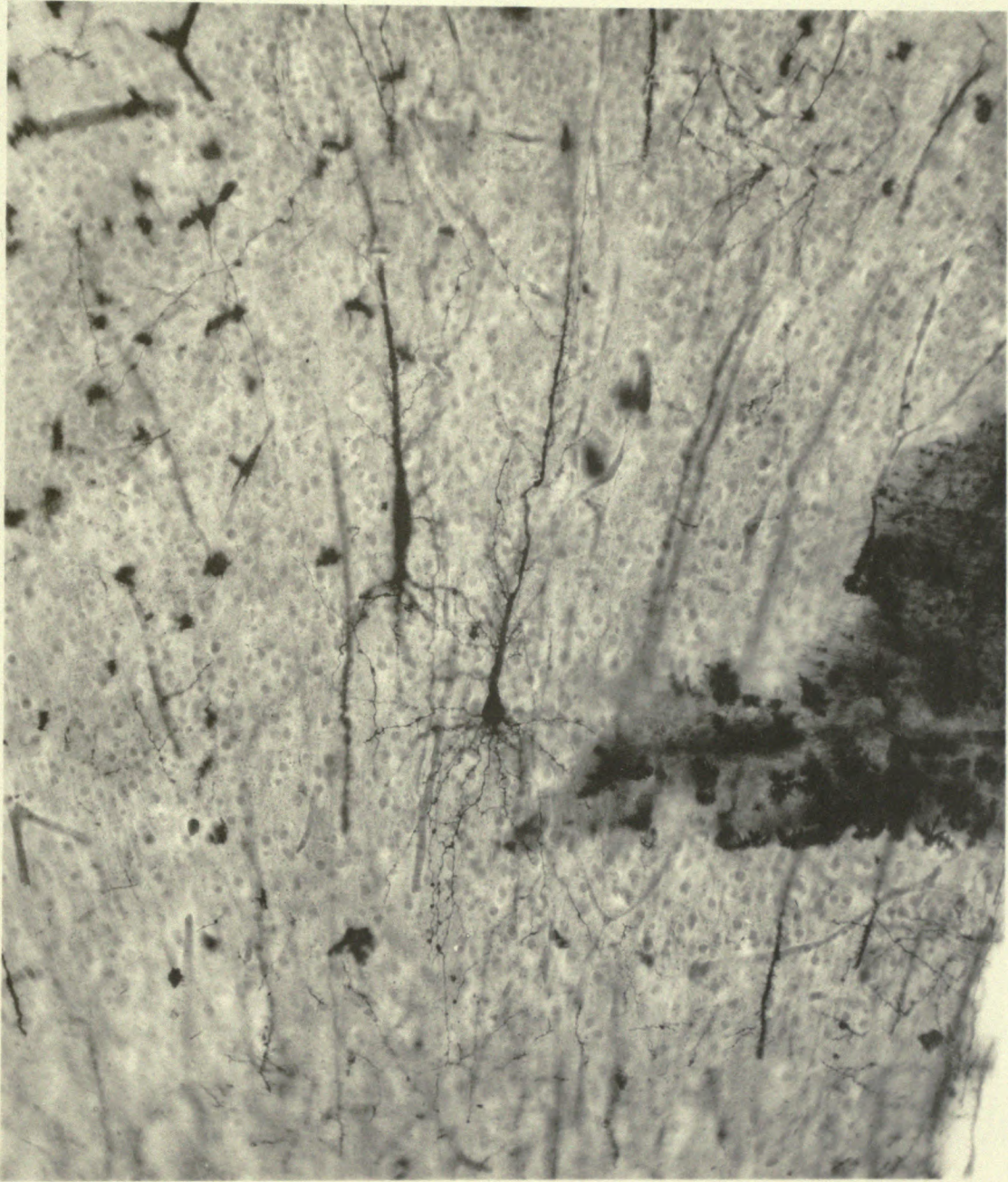
PLATE XLIII.

MEDIUM SIZED PYRAMIDAL CELLS OF THE THIRD LAYER OF THE CORTEX IN HUMAN EMBRYO
SHOWING LONG APICAL PROCESS ENTERING SUPERFICIAL LAYER AND FINE NEURAXON COMING OUT
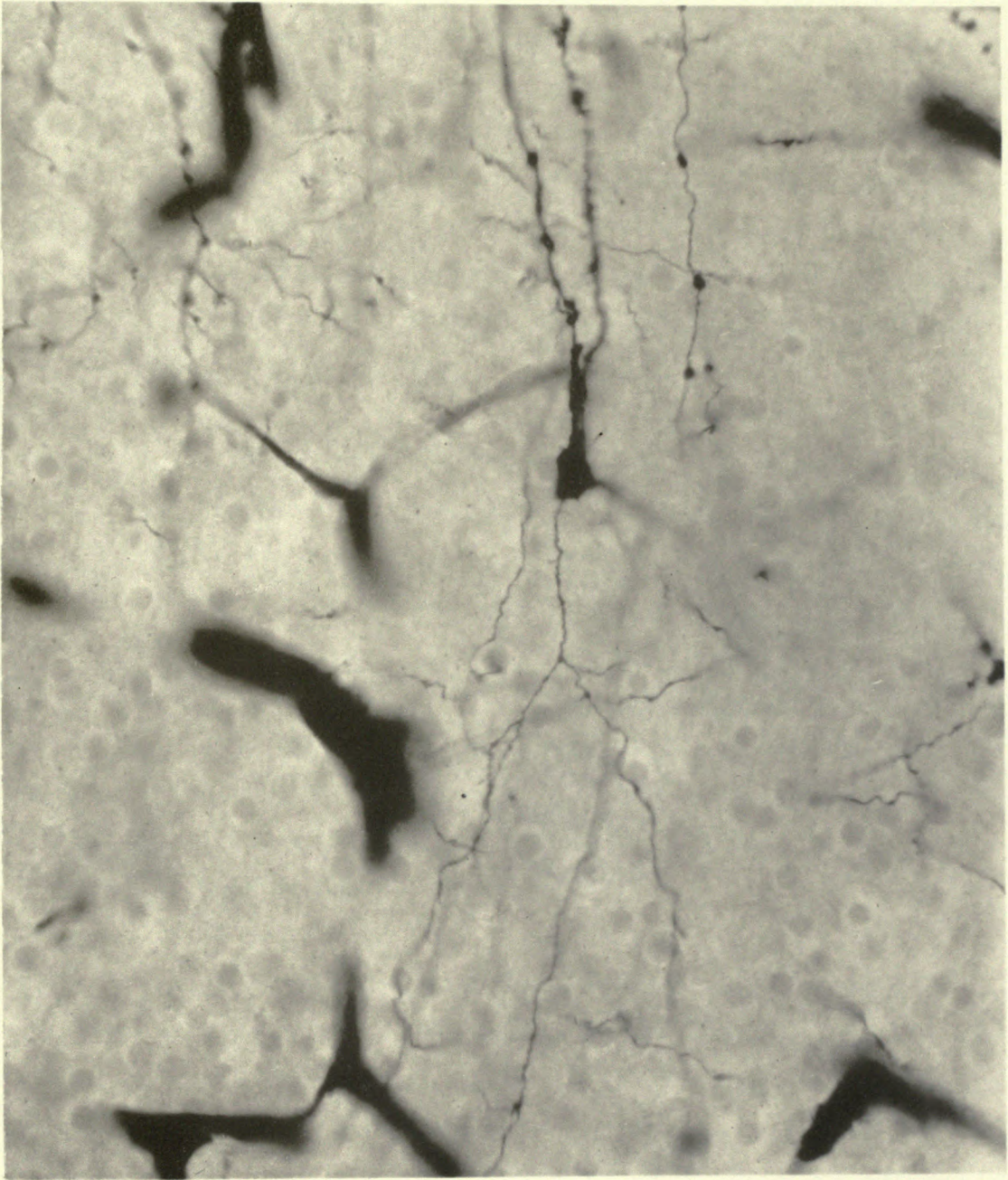OF THE BASE.   X 190 DIAM.

PLATE XLIV.

LARGE PYRAMIDAL CELL OF GOLGI'S SECOND TYPE IN THE THIRD LAYER WITH LONG APICAL PROCESS AND NUMEROUS FINE DENDRITES. THE NEURAXON DIVIDES AND SUBDIVIDES BELOW THE CELL BODY.

PLATE XLV.

A LARGE CELL OF THE THIRD LAYER WITH ITS NEURAXON COMING OUT FROM THE BASE AND DIVIDING INTO TWO BRANCHES WHICH SUBSEQUENTLY DIVIDE. THIS IS AN EXAMPLE OF THE SECOND TYPE OF GOLGI CELL.   X 570 DIAM.

PLATE XLVI.

fine straight fibres, with bead-like swellings at regular intervals, are to be seen extending through the layer. These are thought by Retzius to be neuroglia fibres.

Plate XLIII. shows another group of pyramidal cells (*g*) with the same characteristics as those in Plate XLII. In this plate the axis cylinder process or neuraxon of several of the cells is well shown. It can be seen to issue from the base of the cell, and to pass downward toward the white matter in a wavy course, and to give off little collaterals here and there, some of which appear to turn backward, as if to ascend. Cajal affirms that some collaterals do turn upward and pass into the superficial layer to ramify among the horizontal fibres. In this plate, also, a varicose neuroglia fibre is to be traced. It will be noticed that in the layer beneath the pyramids, where no cells are stained, there are many more fibres of horizontal direction than in the second layer.

Plate XLIV. shows the characteristics of the pyramidal cells already described. The neuraxon of the cell in the centre of the plate is well shown, and the very great difference in its appearance from that of the dendrites is to be noticed. A small collateral is seen to come off from this neuraxon near to the lower limit of the plate.

Plate XLV. shows another pyramidal cell of medium size from the third layer (*k*). It is given in order to demonstrate the branches which often come off from the apical process and ascend at its side. It also shows the divisions and subdivisions of the dendrites given off from the body of the cell, and the tendency to varicose swellings along these dendrites, particularly at the point at which a branch is given off.

In Plate XLVI. a single pyramidal cell is shown with its axis cylinder or neuraxon under a very high power of magnification. This is seen to run from the base and to divide into two branches; each branch then divides, and from these branches smaller collaterals are given off. This cell is one of the cells of Golgi's second type, in which the axis cylinder has no long course or definite destination, but loses itself in a plexus of very fine nerve fibres. It was impossible to focus both cell and fibre upon the plate at once, with this very high power, hence the cell is not clearly shown.
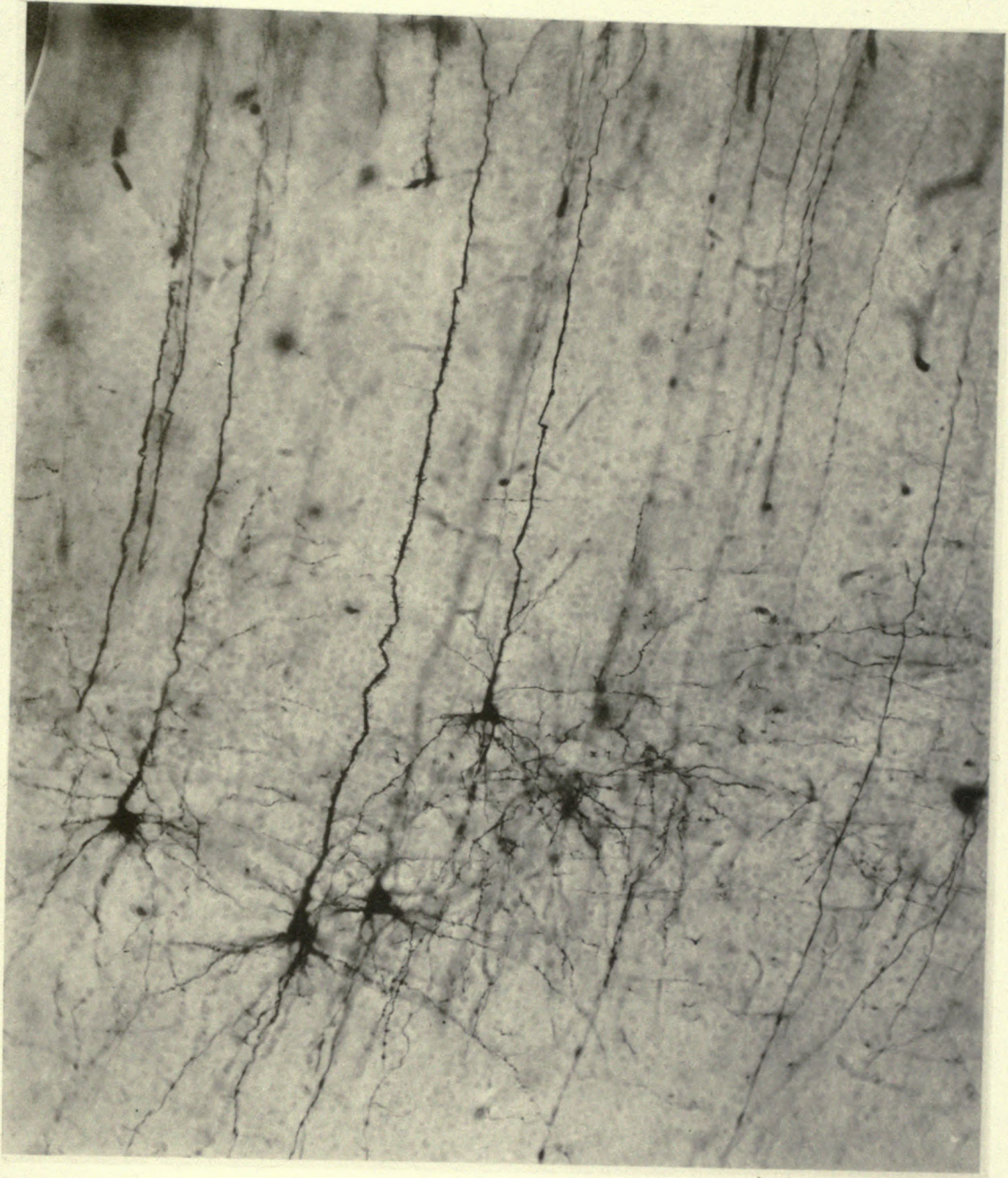
Plate XLVII. shows three of the large pyramidal cells of the cortex (*g*). In this plate the existence of thorn-like excrescences upon the apical process of the cell is clearly shown. These are the so-called gemmules, and it will be noticed that many of them have club-shaped extremities. These gemmules are similar to those already seen on the branches of the Purkinje cells of the cerebellum. Their exact significance is unknown, but Berkley considers them of great functional importance, and has shown[1] that in degenerative diseases of the brain of toxic origin, they are the first part of the cell to suffer, the degenerated cell having a swollen apical process without gemmules. In this plate the division of the apical process and the divergence of its branches before they enter the superficial layer are well seen.

To the right of the plate a long straight neuraxon is seen passing toward the superficial layer. This may be taken as one of the terminal fibres of which so many come up from the cord and basal ganglia and end in the cortex. These, of course, pass between and interlace with the other systems of fibres already described, and make up a considerable part of the white matter. The terminal filaments of these fibres and the terminals of their collaterals enter into close relation with the cells of this layer, and they may thus bring in impulses from a distance, which, being received in the pyramidal cells, set up new responses in the form of motor or sensory or mental activity.

[1] The Medical News; Nov. 9, 1895.

LARGEST PYRAMIDAL CELLS OF THE THIRD LAYER OF THE CORTEX SHOWING LONG APICAL
PROCESS WITH GEMMULES AND NUMEROUS BASAL DENDRITES.   X 190 DIAM.
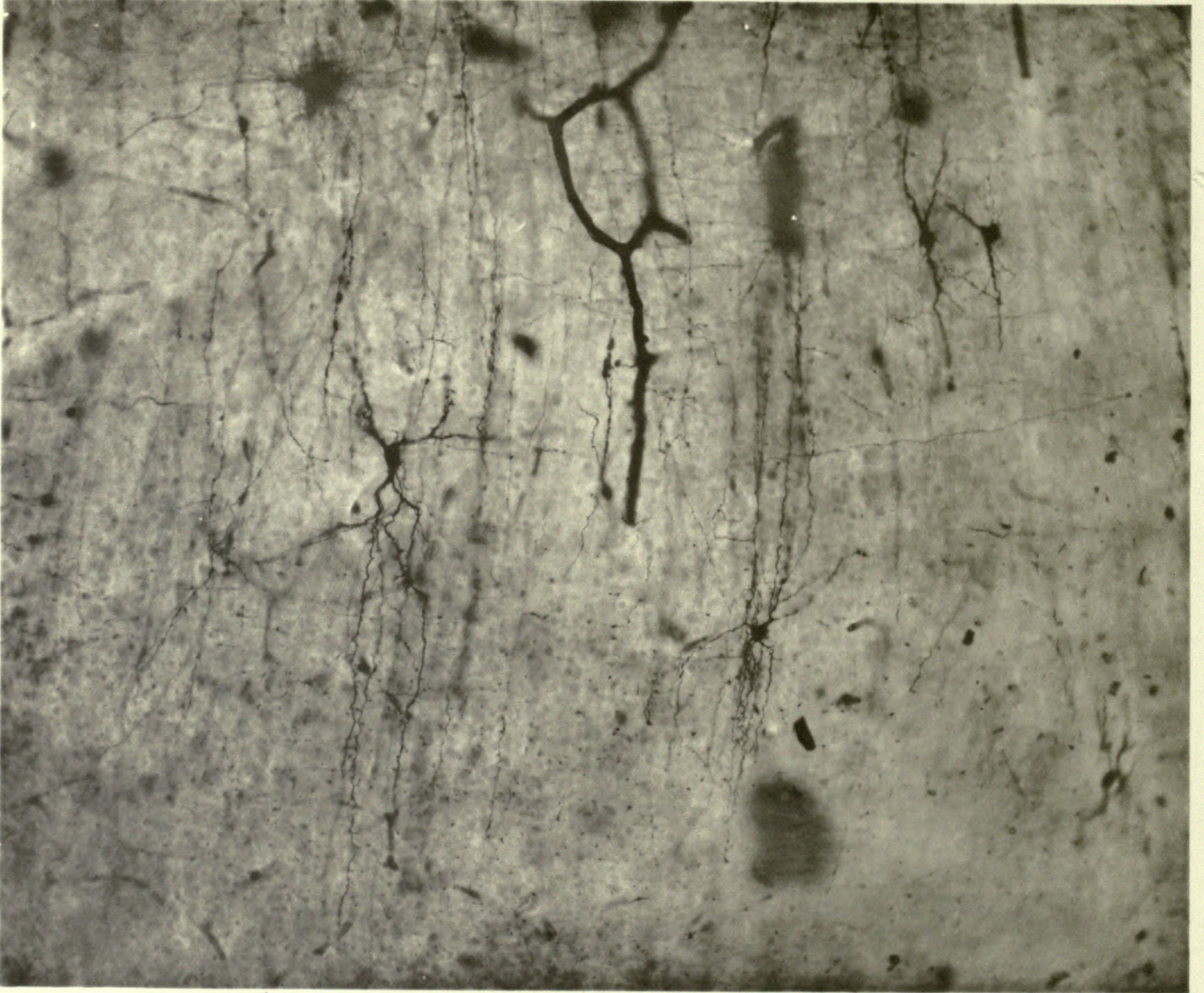
PLATE XLVII.

A MARTINOTTI CELL OF THE THIRD LAYER OF THE CORTEX SHOWING THE AXIS CYLINDER COMING OFF FROM THE APEX AND ASCENDING TOWARD THE SUPERFICIAL LAYER GIVING OFF A COLLATERAL. OTHER AXIS CYLINDERS WITH COLLATERALS ARE SEEN IN THE SECTION. THE STELLATE CELL TO THE LEFT IS A GLIA CELL. X 190 DIAM.

PLATE XLVIII.

THIRD LAYER OF THE CORTEX SHOWING IRREGULAR POLYGONAL CELLS WITH MANY DEN-
DRITES WHICH LIE AMONG THE PYRAMIDAL CELLS.   X 190 DIAM.

PLATE XLIX.

Plate XLVIII. shows the existence of another type of cell found in the third layer of the cortex, and first described by Martinotti (*m*). This variety of cell gives off an axis cylinder from its apex which ascends toward the superficial layer of the cortex, a direction exactly opposed to that of the neuraxon of the pyramidal cells. This axis cylinder gives off collaterals which pass laterally into the adjacent substance. These cells have numerous dendrites which come off from the lower part of the cell body and pass downward, dividing and branching, and furnished with gemmules like the apical process of the pyramidal cell.

The cell to the left of the plate is a glia cell. The numerous branches of such a cell and its spider-like appearance are apparent. The broad black lines are capillaries.

Plate XLIX. shows several cells of irregular type which are found in the third layer of the cortex. They differ in shape from the pyramidal cells. They do not have an apical process, but have numerous long, slender dendrites, and the neuraxon is not easily separated from the dendrites. It is possible that these cells belong to Golgi's second type of cell whose neuraxons divide and subdivide within the cortical layers (*n*).
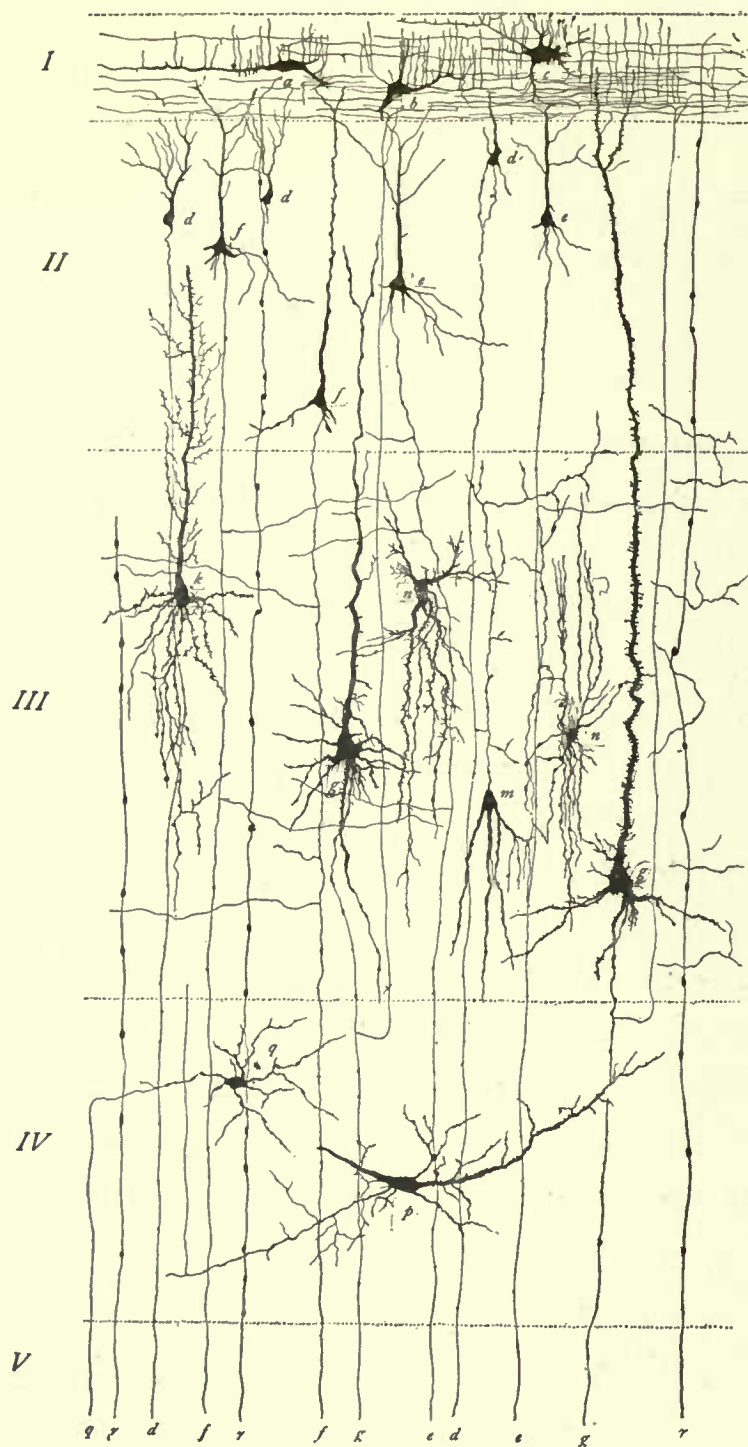
FIG. 10.

THE FOURTH LAYER, OR LAYER OF POLYGONAL CELLS

Plate L. shows the fourth or deepest layer of the cortex. This layer is made up of polygonal or fusiform cells, whose general direction is at right angles to the pyramidal cells of the third layer. One such cell is shown in the plate, a fusiform cell (*p*), its long axis being horizontal. It has two large protoplasmic processes covered with gemmules and giving off branches. It has a large neuraxon which passes almost horizontally toward the left, giving off collaterals, and then turns downward. This cell is rather larger than the majority of the cells of this layer. But other cells of the layer are triangular, rectangular, or polygonal (*q*), hence the latter name has been selected as descriptive of them. Cajal says that a stalk is often wanting in these cells, but when present it varies greatly in its direction, and never turns downward or upward or terminates in the superficial layer of the cortex. The neuraxons of these cells turn downward into the white substance.

All anatomists have distinguished this

FIG. 10. — Diagram of the cells of the cerebral cortex. The cells are reproduced from the plates.

I, superficial layer. *a*, fusiform, *b*, triangular, *c*, polygonal cells of Cajal.

II, layer of small pyramids. *d*, smallest, *e*, small, *f*, medium-sized pyramids with their neuraxons descending to the white matter, giving off collaterals in their course.

III, layer of large pyramids. *g*, largest (giant) pyramidal cells. *k*, large pyramidal cell with very numerous dendrites. All pyramidal cells are seen to send long apical processes up to *I*. *m*, Martinotti cell with descending dendrites and ascending neuraxon. *n*, polygonal cells.

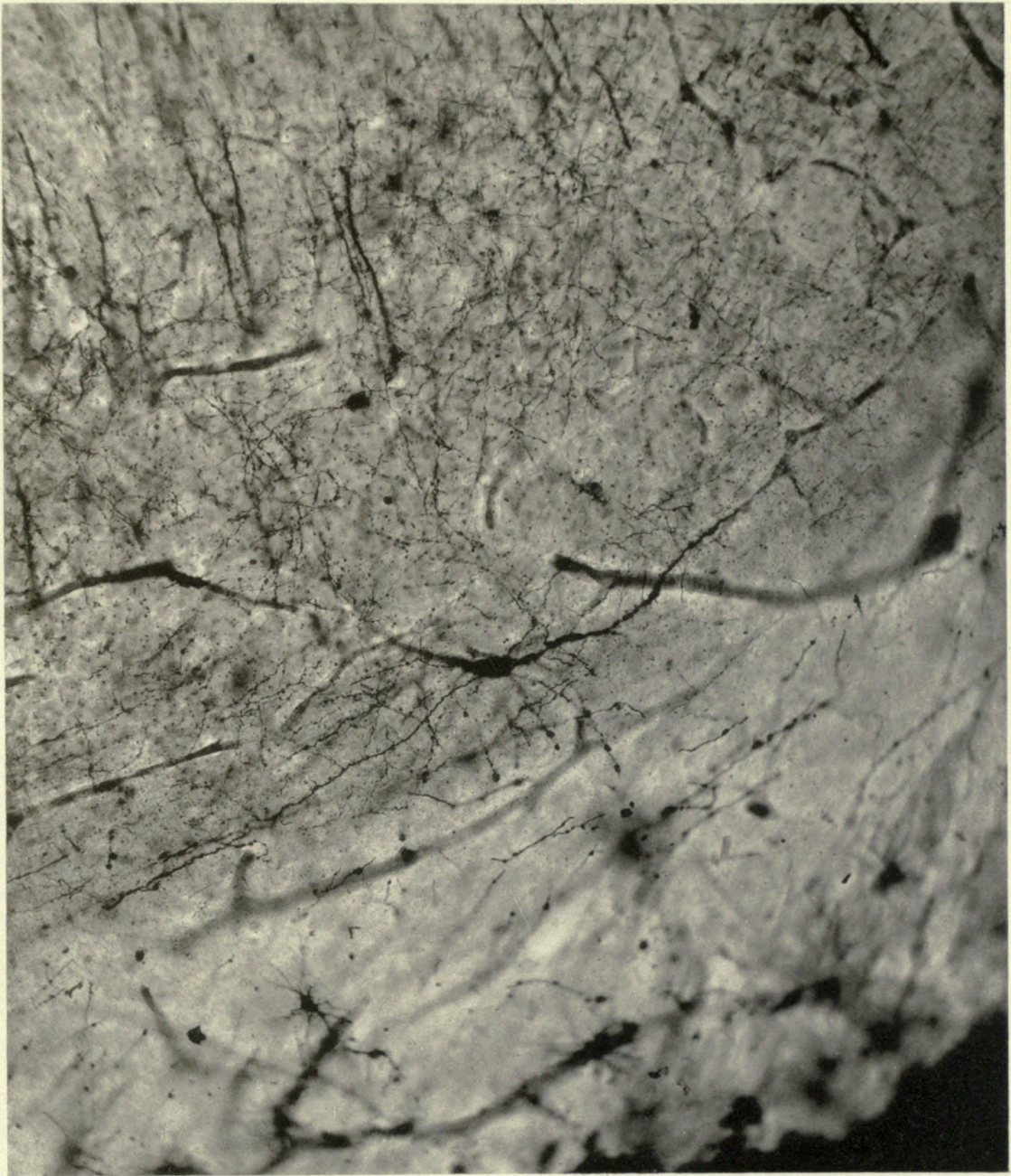*IV*, deep layer. *p*, fusiform cell. *q*, polygonal cell.

V, the white matter containing the neuraxons from pyramidal cells, *d*, *e*, *f*, *g*, and from cell of the deep layer *q*. *r*, neuroglia fibre.

FUSIFORM CELL OF THE FOURTH LAYER OF THE CORTEX; ITS LONG AXIS DIRECTED HORI-
ZONTALLY WITH NUMEROUS DENDRITES AND A NEURAXON PASSING TOWARD THE LEFT.   X 190 DIAM.

PLATE L.

deeper layer of the cortex from the other layers, and have considered its cells as association rather than projection cells. The fibres of this layer are seen to pass in all possible directions, intermingling with the neuraxons of the other layers, which descend through the layer to enter the white matter beneath.

An attempt has been made to put together the various elements of the cortex here described in a scheme or diagram (Fig. 10) which may convey to the mind a picture of their mutual relation. Each variety of cell which has been described and photographed in the plates is reproduced and is given its proper size and position relatively to the other cells. The course of the fibres within the cortex is also shown, with their probable termination so far as actually determined. Fibres *r* are supposed to be glia fibres forming a part of the glia framework supporting the cortex. The various systems of fibres entering and terminating in the cortex are not shown.

FIG. 11.

FIG. 11.—The projection tracts joining the cortex with lower nerve centres. Sagittal section showing the arrangement of tracts in the internal capsule.

A, Tract from the frontal lobe to the pons, thence to the cerebellar hemisphere of the opposite side. *B*, motor tract from the central convolutions to the facial nucleus in the pons and to the spinal cord; its decussation is indicated at *K*. *C*, sensory tract from posterior columns of the cord, through the posterior part of the medulla, pons, crus, and capsule to the parietal lobe. *D*, visual tract from the optic thalamus (*OT*) to the occipital lobe. *E*, auditory tract from the corp. quad. post. to which a tract passes from the VIII. N. nucleus (*J*) to the temporal lobe. *F*, superior cerebellar peduncle. *G*, middle cerebellar peduncle. *H*, inferior cerebellar peduncle. *CN*, caudate nucleus. *CQ*, corpora quadrigemina. *Vt*, fourth ventricle. The numerals refer to the cranial nerves.
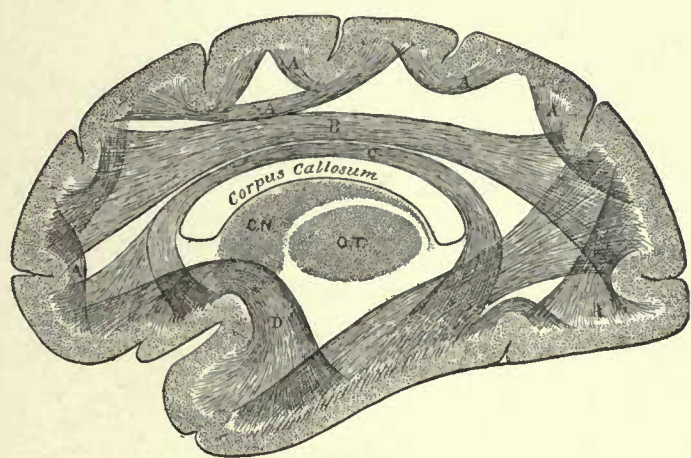

FIG. 12.

FIG. 12.—The association fibres.

A, Between adjacent convolutions. *B*, between frontal and occipital areas. *C*, between frontal and temporal areas, cingulum. *D*, between frontal and temporal areas, fasciculus uncinatus. *E*, between occipital and temporal areas, fasciculus longitudinalis inferior. *CN*, caudate nucleus. *OT*, optic thalamus.

The neuraxons of all these cells are shown, making up the white matter beneath the gray, and giving off in their course collaterals which pass in various directions.

The various neuraxons making up the white matter beneath the cortex have been classified by anatomists in accordance with their final destination.

There are (1) *projection fibres*, which pass through the centrum ovale into the internal capsule and thence to some of the masses of gray matter in the basal ganglia, medulla, or spinal cord. These bring the

cortex into relation with the lower levels of the nervous system, the various parts of which have been already studied. They are shown in Fig. 11.

There are (2) *association fibres*, which pass from one part of the cortex to other parts, thus bringing various regions of the cortex into mutual relation. They are shown in Fig. 12.

There are (3) *commissural fibres*, which pass by way of the corpus callosum from the cortex of one hemisphere of the brain to the opposite hemisphere, to terminate in the cortex.

It is not at all impossible, in the light of recent discoveries, that a neuraxon from a nerve cell may become a projection fibre and give off collaterals, which may become association or even commissural fibres. It is certain that the human brain is superior to that of all other brains in the number of its association fibres which bring about a perfect interaction of all its parts. The termination of these association fibres appears to be in all of the various layers of the cortex, thus bringing any cell into relation with many cells of different situation and type.

It has been stated already that the cortex is the terminal station of a very large number of fibres which reach it from other parts — in the projection, association, and commissural tracts. These fibres are not shown in the diagram (Fig. 10), for the sake of clearness, but they are shown in Fig. 13 from a design by Andriezen[1] which demonstrates their complexity. They enter the
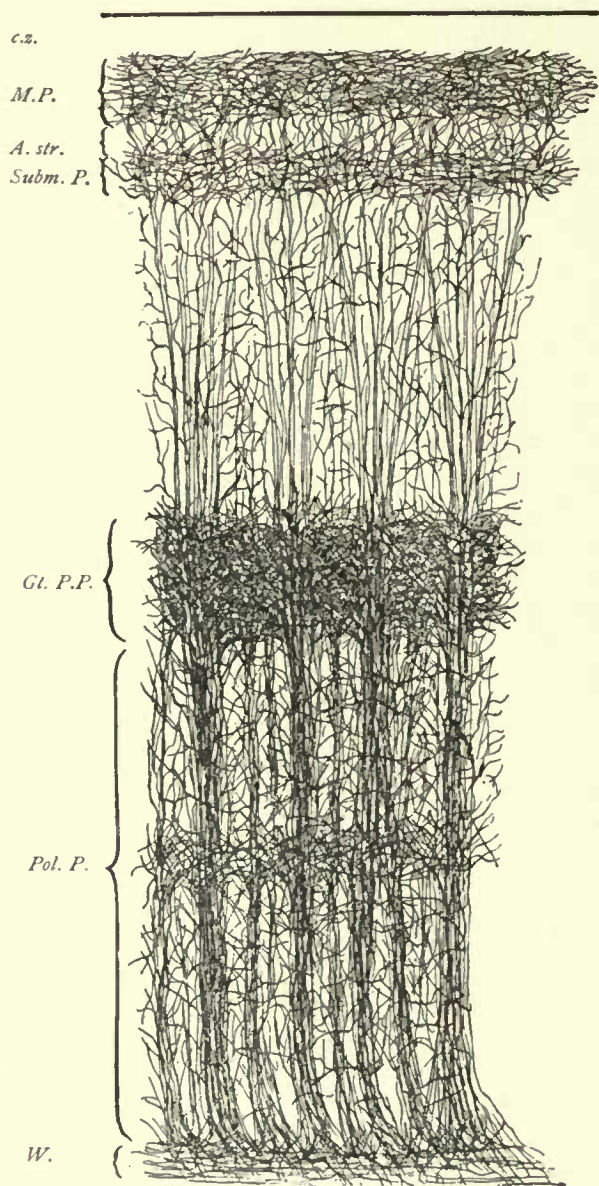

FIG. 13.

FIG. 13. — (Andriezen). Cortex of human brain showing the nerve fibre systems and plexuses (combined Weigert's and Golgi's methods).

c z, clear zone (free of nerve fibre). *M P*, molecular plexus (Exner's), in the molecular layer. *A str*, ambiguous cell stratum. *Subm P*, sub-molecular plexus. *Gt PP*, great pyramidal plexus. *Pol P*, polymorphic plexus. *W*, white substance.

cortex from the white matter and terminate in brush-like expansions about the cells of all the various layers. At some layers the intricate meshes of these fibres are very thick. The

[1] Brain, Vol. XVII. p. 629; 1894.

thickest meshes are about the bodies of the largest pyramid cells and of the fusiform cells of the deep layer. Many fibres ascend to the superficial layer, where a larger mesh is shown to exist about the Cajal cells. There are terminal ends of fibres at all parts of the cortex, and — as Andriezen has pointed out — these are non-medullated at their tips, where they can come into contact with the dendrites and apical processes of the cortical cells. An attempt has been made by Cajal[1] to trace the probable course of impulses through the various cortical layers, but such an attempt is too hypothetical to be at present considered.

[1] Cajal, Les nouvelles Idées sur la structure du Système Nerveux, p. 66. Paris, 1894.

The Hippocampus

The hippocampus is a peculiar structure which has attracted the attention of all anatomists who have studied the brain. It lies deep upon the base on the inner surface of the tempero-sphenoidal lobe, its free inner surface projecting into the descending horn of the ventricle. The peculiar appearance of the anterior portion known as Ammon's Horn is due to a folding of the convolution upon itself in such a manner that the outer layer of one portion of the cortex, being folded backward, comes in contact with the outer layer of another portion of the cortex, and the free extremity is rolled outward in a sort of spiral curve. This peculiar configuration is well shown in Plate LI.

It is not necessary to give a very detailed account of this structure, as its physiological significance is not yet known. It is much more fully developed in the lower animals than it is in man. It is easily possible to distinguish a number of layers in the cortex, and these may be enumerated as follows (from right to left in the figure):

First. A layer of epithelium upon which lies the choroid plexus in the descending horn of the lateral ventricle. This forms the outer boundary of the alveus.

Second. The second layer is the layer of white matter, really made up of the neuraxons issuing from the base of the pyramidal cells, but deflected by the curving of the convolution into a zone of horizontal fibres. This is known as the Alveus.

Third. A thin layer containing numerous polygonal cells which are similar to those of the fourth layer of the cortex. This has been called the stratum oriens.

Fourth. A layer of pyramidal cells of various shapes and sizes having many dendrites and long apical processes which divide and branch as they enter the fourth layer. This corresponds to the third and second layers of other cortical regions fused together.

Fifth. A layer made up of numerous fine fibres passing in all directions, and of many cells. This is really the superficial layer of the cortex, and is fused with a superficial layer of the other part of the cortex, which is folded upon this layer; so that this broad layer represents the union of two superficial cortical layers. It has been named the stratum lacunosum. It contains many Cajal cells and cells of Golgi's second type.

Sixth. A layer of pyramidal cells with their bases directed away from the layer of fine fibres; thus lying in exactly an opposite direction to the cells of the fourth layer.

Seventh. A layer of white matter made up of the neuraxons coming out of the base of these pyramidal cells. The fibres issuing from the seventh layer gather into a mass and

A SECTION THROUGH THE HIPPOCAMPUS OF AN EIGHT MONTHS HUMAN EMBRYO, SHOWING
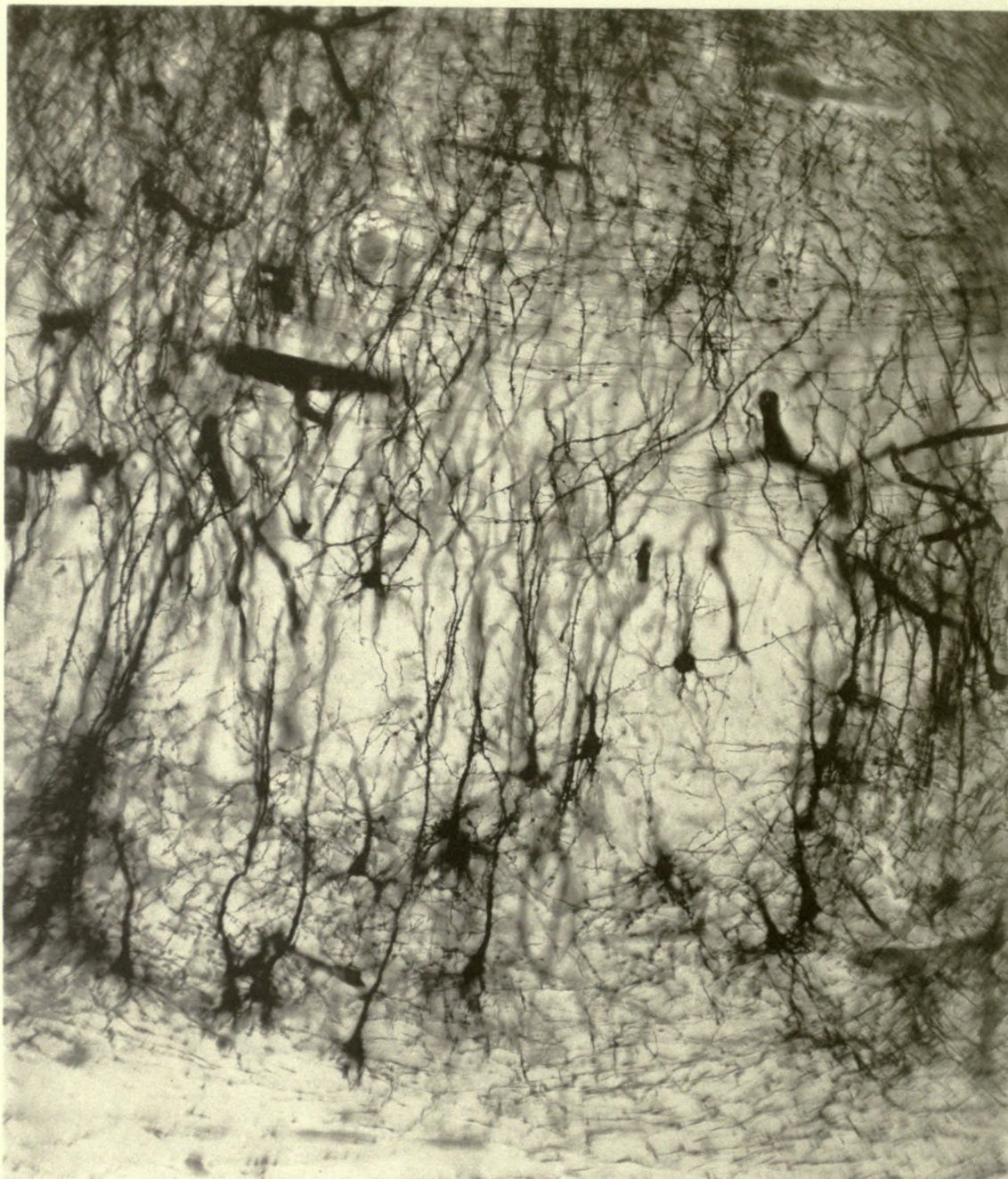VARIOUS LAYERS OF THE CORTEX.   X 29 DIAM.

PLATE LI.

THE CORTEX OF THE HIPPOCAMPUS. THE LONG PYRAMIDAL CELLS, THE SMALL PYRAMIDAL
CELLS AND THE INTERLACING LAYER OF FINE FIBRES ARE ALL EVIDENT.   X 190 DIAM.

PLATE LII.

sweep around the free extremity of gray matter, and thus arrive upon its surface, there passing beneath the layer of epithelium. Hence the layer of white matter which we have described as the second layer of the hippocampus is really made up not only of the neuraxons issuing directly into it from the first set of pyramids described, but also contains fibres coming from the second set of pyramids by a long spiral curve.

It is possible in the plate to follow the layer of pyramids all the way around the curve of the cortical fold, and thus to become convinced that this layer of pyramids is really a single layer folded upon itself, and hence necessarily lying with all the bases outward.

Plate LII. shows a section through the hippocampus at a higher power. At the bottom of the plate the layer of white substance is seen, with a few fibres passing chiefly in a horizontal direction. Above this layer the pyramids lie with their long apical processes, similar in appearance to those which we have already studied. These apical processes are seen to divide and enter the layer of fine fibres, where they interlace with the fine horizontal fibres of the superficial layer of the cortex. These fine fibres are quite easily visible in the plates. In the ordinary cortex the superficial layer is comparatively thin, and the apical processes of the pyramids diverge and become parallel with the surface soon after their entrance into it; but in this region it is evident that the layer of tangential fibres is broad, and that there is less tendency of the apical processes to become horizontal. The interlacing of the two sets of fibres in this layer is well demonstrated in the plate. In the plate a few small cells can be seen in the superficial layer. These have been termed stellate cells by Cajal. They have numerous dendrites which branch and interlace with the other fibres of this layer adding to its complexity. Dejerine[1] describes other fibres entering and branching in this layer which are terminal collaterals from the cells of the other layers. It will be noticed that no distinction has been made between the layer of small pyramids and the layer of large pyramids in this description of the hippocampus. No such distinction is possible, because the cells are intermingled.

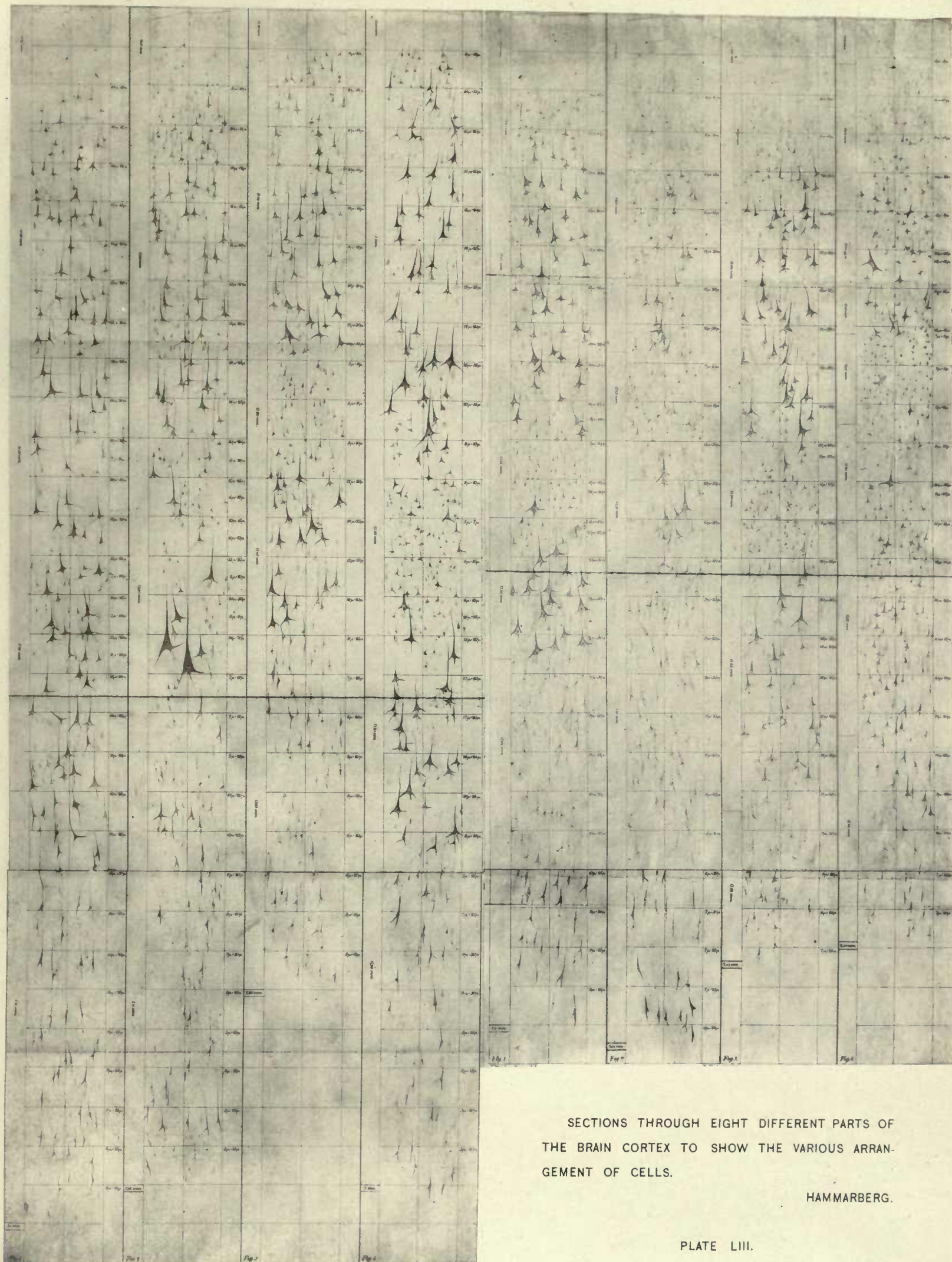[1] Anatomie des Centres Nerveux, p. 722. Paris, 1895.

In the description of the cortex given above it has been described as consisting of four layers. It is easily possible to distinguish everywhere in the cortex the four types of cells described in these layers; viz. Cajal cells, small pyramidal cells, large pyramidal cells, polygonal cells. But the relative number of these cells varies greatly in different regions of the brain, and their arrangement in layers also varies. Thus few authors have agreed as to the number of layers of cells to be described, and it is erroneous to suppose that any single scheme corresponds to all parts of the brain. Bevan Lewis has shown some of the differences existing in the cortical structure in different regions (see Quain's "Anatomy," 10th edition). But the most careful study was made by the late Dr. Carl Hammarberg of Upsala, in "Studien über Klinik und Pathologie der Idiotie nebst Untersuchungen über die Normale Anatomie der Hirnrinde," and his plates are reproduced in Plate LIII.

Hammarberg's drawings of sections through various parts of the cortex made to a scale have proven that great variations in number and arrangement of the cells exist, that the frontal, parietal, central, occipital, temporal, and median portions of the brain as well as the gyrus fornicatus and the hippocampus have distinctive characteristics, and that no description of one portion holds good for all. It is beyond the scope of this work to describe these variations, which are rather in the mutual relation of such cells as have been shown than in any peculiarities of cell structure. It has seemed necessary, however, to observe that the four-layer type of structure is by no means universal, and should not be taken as typical of cortical structure in man, however universal in lower animals.

Plate LIII. shows sections from eight different regions of the adult human cortex, drawn to a scale, and demonstrates the varying thickness of the cortex and the varying arrangement of the cells in different parts. The first four sections are from the anterior regions of the brain, and present the appearances supposed to characterize the motor cortex. They are from the superior frontal (Fig. 1); anterior central (Fig. 2); third frontal, posterior to the ascending limb of the fissure of Sylvius (Fig. 3); third frontal, anterior to the ascending limb of the fissure of Sylvius (Fig. 4). The second four sections are from the posterior regions of the brain, and show the arrangement of cells prevailing in the sensory areas of the cortex. They are from the posterior central (Fig. 1); superior temporal (Fig. 2); superior parietal (Fig. 3); and superior occipital (Fig. 4). It will be noticed that the larger pyramidal cells are found more constantly in the motor region, and that the contrast between layers of large and small cells is more apparent in the sensory region. It is as yet impossible to assign any separate functions to the various kinds of cells. Hammarberg's studies, however, demonstrate conclusively that the degree of mental power depends directly upon the number and perfection of development of these cortical cells, for in the brains of idiots the cells are few in number and imperfectly developed.

SECTIONS THROUGH EIGHT DIFFERENT PARTS OF
THE BRAIN CORTEX TO SHOW THE VARIOUS ARRAN-
GEMENT OF CELLS.

HAMMARBERG.

PLATE LIII.